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# Residential Development and Environmental Weeds in Indigenous Forest Patches, Otatara, Southland.

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# Abstract

Residential development is widely perceived as a threat to indigenous vegetation and habitat. New Zealand lowland forests, which have been extensively fragmented and modified since colonisation, may be particularly vulnerable. Increased exotic plant invasion of forest remnants is a potential result of nearby residential development. Environmental weeds cause loss of biodiversity at genetic to ecosystem levels of organisation. The impact of residential development was examined in podocarp forest remnants in a matrix of rural and residential land at Otatara, Southland. Correlation between abundance of exotic plants and population density or degree of development has been observed at coarse scales in many areas but few studies have examined mechanisms underlying this pattern. Residential development is thought to exacerbate weed invasion by increasing the likelihood of exotic plant propagules entering forest remnants and by changing conditions within the forest to aid exotic plant establishment and growth.

Field data was collected along transects from the forest edge into the interior for 13 study sites at Otatara. The abundance of environmental weeds was quantified at intervals along each transect. Indicators of the spatial context: distance of each quadrat from the forest edge; age of residential development and number of known weed species growing on the adjoining property, and edge structure and three environmental characteristics of the forest: light availability, soil fertility and degree of anthropogenic disturbance, were also assessed. The field data was examined using bivariate correlation analysis and multivariate regression. Weed abundance within forest was significantly correlated to light availability, degree of anthropogenic disturbance, and to distance in from the forest edge and edge structure. Even though a significant correlation was not found between weed abundance and age of residential development (perhaps because of the small scale at which this research was conducted), the factors that are correlated to weed abundance are altered by residential development in ways expected to facilitate weed invasion. Thus, it seems likely that nearby residential development exacerbates weed invasion. Maintaining a relatively closed edge structure and minimising disturbance within forest may lessen this effect.

Key words: environmental weeds; urbanisation; landscape ecology; forest fragmentation; Southland, New Zealand.

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# Chapter 1

# Introduction

Deforestation, ecosystem fragmentation and urbanisation are land use changes occurring in many parts of the world (Hobbs, 2000). Destruction of forest and woodland communities has traditionally been associated with land clearance for agriculture but, especially in developed countries, is increasingly related to residential development (Swetnam et al., 1998). Habitat loss and degradation is widely seen as the primary threat to global plant diversity, followed by the effects of invasive taxa (Hayden Reichard and White, 2001).

Fragmentation is an aspect of habitat loss theorised to have deleterious effects on biodiversity, including loss of indigenous species and changes in community composition and ecosystem function (Saunders et al., 1991). It has been the subject of considerable research (reviewed by Bunnell, 1999; Debinski and Holt, 2000). A particular issue for research, and for conservation management, is invasion of indigenous habitat by exotic plants and animals; as fragmentation increases the ratio of edge to interior habitat so there are more opportunities for edge specialists and adventive exotic species to become established. Residential development can exacerbate this, by increasing the load of exotic species in the matrix around habitat fragments and changing habitat conditions - increased human population densities typically lead to increased disturbance of indigenous communities.

The problems caused by development and forest fragmentation are significant in New Zealand, where numbers of suburban and lifestyle properties in once rural land are increasing, particularly around urban centres (MfE, 2000). This threatens the patchy remnants of New Zealand's once extensive lowland forests, which support a disproportionate amount of national biodiversity, are often unprotected, and vulnerable to the effects of invasive species (Clout and Saunders, 1995). Effective conservation requires understanding of the impact of such development on New Zealand's biota, particularly in lowland forest ecosystems. This thesis responds to that need.

A committee investigating issues of conservation on private land noted:

> [A] land use change with significant implications for indigenous biodiversity is urban growth and small-lot (principally peri-urban) development. Intensification of land use, whether for residential purposes or intensive production uses, is most common in fertile lowland and coastal areas. It is these same areas that originally hosted the greatest diversity of species and now contain some of New Zealand's scarcest habitats ... development in these locations inevitably stresses already delicate and highly fragmented systems.
>
> Data detailing the specific effects on biodiversity from urban development is not available for New Zealand... (MfE, 2000b p26)

The widespread belief that residential development may 'stress' forest remnants is rests largely on theories of landscape ecology, which may not be supported by empirical data. This thesis examines one potential effect of urban development on biodiversity: the relationship between residential development and environmental weed invasion of lowland forest stands at Otatara, Southland. Several studies provide evidence that increased weed abundance is associated with residential development, but these are often conducted at coarse scales. Few examine specific mechanisms by which residential development might enhance weed invasion.

## 1.1 Weed invasion and landscape ecology

Several strands of research inform this study. Firstly, broad scale or conceptual studies of the structure of landscapes, and how different elements of the landscape may interact (for example Collinge, 1996; Medley et al., 1995) form a framework for hypothesising ways by which residential development may affect indigenous forest. Secondly, there are detailed studies of weed invasion: attempts to identify the traits that allow exotic plants to become successful weeds (for example, Goodwin et al., 1998), and attempts to explain the distribution of weeds by reference to biological characteristics of species and the environmental features of a particular habitat, which may include such 'landscape elements' as disturbance patterns (for example Buist et al., 2000; McCay, 2000).

An emerging body of research combines those strands, relating abundance of weedy species (often using species richness as the dependent variable) to environmental conditions, including explicit consideration of landscape elements or spatial context (Burke and Nol,

1998; Harrison et al., 2001; Rose and Fairweather, 1997). However, this literature rarely concerns the effects of changes in land use, especially in New Zealand.

The plant invasion literature is reviewed later (Chapter 2), but this introduction will explain why landscape ecology can usefully inform weed research. Landscape ecology is concerned with the spatial patterns of ecological entities and processes (Kupfer, 1995; Pickett and Cadenasso, 1995; Swetnam et al., 1998) and is relevant to the present study for two reasons. Firstly, it is useful for conservation planning in areas where indigenous species and communities are juxtaposed with economic land uses (Collinge, 1996). Secondly, it is relevant to analysis of weed invasion because the process of a species spreading into a new area is inherently spatial (Cadenasso and Pickett, 2001).

### 1.1.1 Interactions between developed land and habitat patches

Habitat fragmentation (reduction in the size and continuity of indigenous habitat) is a common consequence of land conversion. Landscape ecology traditionally used the equilibrium theory of island biogeography and meta-population models of population dynamics to describe the outcomes of this process (Bunnell, 1999). The equilibrium theory of island biogeography posits that the number of species present on an island is determined by the size of an island and its distance from a source of potential colonists: nearer and/or larger islands support more species (Gilbert, 1980). This simple model does not seem to apply to weed invasion of habitat 'islands' in a developed matrix (Gilfedder and Kirkpatrick, 1998). Landscape ecology has supplemented those basic principles with sophisticated descriptions of interactions between the matrix and remnant habitat (Collinge, 1996; Kupfer, 1995). For instance, it is generally accepted that habitat conditions at a border between indigenous vegetation and cleared land differ from those of interior forest because the former is influenced by environmental conditions of the surrounding area, the matrix (Saunders et al., 1991). Characteristics of the matrix (Mesquita et al., 1999) and the structure of the patch edge also determine the influence of external conditions on the habitat interior (Murcia, 1995).

The effect of residential development - as a change in the landscape structure - has been the subject of considerable research (Matlack, 1997; Medley et al., 1995; Norton, in press). Many studies have described effects on wildlife, particularly birds. It is consistently noted that the abundance of some species decreases as human modification of the landscape intensifies (Rottenborn, 1999) and overall diversity decreases (Cam et al., 2000). Those

changes occur even if habitat patches are left intact and development takes place in the periphery (Rottenborn, 1999). In general, development is thought to have negative impacts on the quality of remaining vegetation and habitat. One commonly mentioned effect is increased invasion by opportunistic animals and plants well adapted to thrive in residential landscapes (Friesen, 1998; MfE, 2000).

### 1.1.2 The spatial nature of weed invasion

Ideas from landscape ecology should be incorporated in studies of weed invasion because the process of weed invasion is explicitly spatial, although this has often been overlooked (Cadenasso and Pickett, 2001; Parendes and Jones, 2000). It is often noted that weeds are more abundant toward the edges of habitat patches (Chapter 2), which implies that either conditions at habitat edges favour weed establishment and growth, or weeds spread into habitat patches from the disturbed matrix and are more abundant close to the edge as the entry point for propagules. In either case, this distribution suggests that environmental qualities of the edge and the surrounding matrix may be determinants of weed abundance within habitat patches (Pickett and Cadenasso, 2000).

There has been limited research into the links between weed invasion and residential or urban development, but available information suggests that development is associated with increased abundance of naturalised exotic species (Batianoff and Franks, 1998; Fensham and Cowie, 1998; Moran, 1984; Rose and Fairweather, 1997; Roy et al., 1999). Few studies have attempted to identify and evaluate the mechanisms that underly this. This thesis uses information from Otatara to create a conceptual model of how residential development may alter the surrounding matrix, the edge, and the forest interior, to cause increased abundance of environmental weeds in indigenous forest patches.

## 1.2 Links between development and weed invasion

Norton (in press) suggested that residential development at Otatara could exacerbate the impact of invasive plants by increasing the extent and magnitude of human disturbance - which creates sites for weed establishment and growth - and by increasing the size and proximity of sources of exotic propagule – which raises chances of dispersal into forest. Those concepts are explored more fully below.

### 1.2.1 Enhanced dispersal

Residential developments may enhance weed abundance in nearby forest stands by increasing the abundance of exotic plant propagules able to disperse into forest. A greater biota of exotic plants is present in developed areas, because species are deliberately introduced in gardens and because adventive species often establish in suburban environments. If more propagules are produced, more are likely to enter the forest and become established.

Residential development may make dispersal more effective. The relative length of edges (the locus of entry points) may be increased, and the structure of edges may be changed, allowing easier penetration. Traffic into forest may increase, because of a rise in local population density, improving chances of transport on human or animal vectors.

### 1.2.2 Sites for establishment

Residential development could facilitate invasion by creating sites with conditions suitable for weed recruitment. Firstly, further fragmentation of the forest and creation of edges (or changes to edge structure) may increase the extent of edge effects, so that environmental conditions - such as light availability - within the forest become more like those of the matrix, thus facilitating weed establishment. Secondly, increased human use of forest will intensify disturbance, which encourages weed establishment (Hobbs and Huenneke, 1992).

The following sections discuss concepts central to this topic, providing a definition of environmental weeds, description of the threat they pose to indigenous biodiversity, and a context for conservation in New Zealand which, if current trends continue, will require better knowledge of the links between development and forest viability

## 1.3 Environmental weeds

The 20th century has seen the rapid loss and extreme fragmentation of natural ecosystems, together with accelerated growth in human population density and expansion international transport. Those changes have enabled the spread of animal and plant species beyond their natural ranges (Ewel et al., 1999). Homogenisation of the world's biota, through spread of species into novel areas, has implications for food production, human health, and conservation (Mack and Lonsdale, 2001; Mooney and Hobbs, 2000). Invasive species are a major threat to indigenous biodiversity, including ecosystem function (Kolar and Lodge, 2001), second only to habitat loss (Ewel et al., 1999).

Ecosystems and communities are dynamic. A species assemblage does not remain static, in an immutable, 'natural' state (Ogden, 1995). Rather, spontaneous range extension is common, and need not adversely affect biodiversity (Lodge, 1993). However, contemporary plant invasions differ from natural range expansion in two important respects. Firstly, ecosystems are rapidly and increasingly being transformed by human activity, so species can spread into habitats normally closed to them by environmental barriers. Secondly, rates of transport of plant propagules have increased globally so that distance no longer hinders their spread (Hayden Reichard and White, 2001; Hobbs, 2000). Humans are primary agents for plant transfer between landmasses, and the species we introduce seem more likely to become weeds than those dispersed by ocean currents or wind (Mack and Lonsdale, 2001). Under those conditions, plant invasions have more potential to alter indigenous vegetation. Introductions may be useful for horticulture or other human activities, and will not be halted, but there is general recognition of the need for better understanding of what facilitates or hinders the spontaneous spread of species into new communities (Ewel et al., 1999).

An introduced plant is not necessarily a weed. Weeds are detrimental to human interest or values (Mack and Lonsdale, 2001; Williams, 1997), and are defined by reference to those values, so it is impossible to classify weeds categorically. Pheloung et al. (1999) asked thirteen experts to classify a set of exotic plant species present in New Zealand as 'major weeds', 'minor weeds', or 'non-weeds'. The groupings were influenced by the expert's affiliation: conservationists and botanists labelled more plants as weeds than did agriculturalists.

This thesis focuses on environmental weeds, which pose a threat to indigenous biodiversity. Cronk and Fuller proposed the following definition of an 'invasive plant', which refers to both the process of invasion and its implications for indigenous biodiversity:

> An alien plant spreading naturally (without the direct assistance of people) in natural or seminatural habitats, to produce a significant change in terms of composition, structure, or ecosystem processes. (1995, p1)

An underlying principle of the equilibrium theory of island biogeography is that a certain habitat can only support a given number of species, and that when a new species colonises that habitat it will lead to the exclusion of a species already present (Gilbert, 1980). This is not always true. Not all introduced species, nor even all naturalised species, that maintain sustainable populations without human intervention, substantially alter indigenous ecosystems (Rejmanek, 2000). Conversely, environmental weeds may be indigenous species that spread into a new habitat and have serious impact on extant species or communities (Williams and West, 2000).

Several authors have defined environmental weeds in a New Zealand context. Williams, for example, referred to "plants that diminish the natural values of the area being invaded" (1997, p6). Williams and West defined environmental weeds as: "plants that invade natural ecosystems and can cause major modifications to indigenous biodiversity and ecosystem function" (2000, p425). Reid refers to "any foreign plant species [inclusive of natives in novel habitats], that threatens local native species or ecosystem processes" (1998, p6). Those definitions encompass the process of invasion and their negative impact on the host community and Reid's will be used in this thesis.

## 1.3.1 Environmental weeds in New Zealand

Extensive clearance and modification of indigenous vegetation - resulting in fragmented and degraded habitat - along with introduced plants and animals have shaped the contemporary New Zealand landscape (DoC and MfE, 2000) and remain principle causes of local decline in biodiversity (MfE, 2000b).

Polynesian colonists introduced a few exotic plants to New Zealand (Atkinson and Cameron, 1993, most of them food plants, like kumara (*Ipomoea batatas*)[1], taro (*Colocasia esculenta*)

[1]Throughout this thesis plants and animals are called by common names. Scientific names are given in italics at the first citation. Nomenclature is after Nicol (1997) for plants and Falla et al. (1981) for birds.

and paper mulberry (*Broussonetia papyrifera*) (McGlone et al., 1994). European colonists introduced many more species (Williams and West, 2000) to be used as food, forage, and ornamental garden plants (Atkinson and Cameron, 1993). It is probable that little attention was paid to their potential to affect on indigenous vegetation, as was the case elsewhere (Ewel et al., 1999). Accidental introductions have also contributed to the number of exotic plants in New Zealand (Williams and West, 2000).

Of the 20 000 plant species introduced to New Zealand, more than 2 000 have successfully naturalized, and approximately 240 are recognised environmental weeds (Williams and West, 2000). Exotic plants are present in all types of indigenous habitat (Lee, 1999). The rate of introductions is increasing (Atkinson and Cameron, 1993) and on average, 11 species become naturalised annually (Craig et al., 2000). New environmental weeds will emerge either from those introductions or from the spontaneous spread of plants already present in small or contained populations (Ewel et al., 1999; Lee, 1999). A plant can become invasive even after some time if circumstances change; for instance, with the introduction of a key pollinator (Hayden Reichard and White, 2001).

New Zealand's indigenous biota evolved in relative isolation, which has increased its vulnerability to introduced pests (Clout and Lowe, 2000). There was no selection for species with strategies to minimise the effects of mammal herbivory, so many indigenous species have been severely affected by introduced mammals (DoC and MfE, 2000). Similarly, evolutionary isolation has increased the vegetation's vulnerability to weed invasion (Williams and West, 2000): competitors and predators that could control population growth in weed species' natural ranges may not be present in the New Zealand biota (Lee, 1999). Indigenous vegetation is also vulnerable because some types of plant, such as nitrogen fixing herbs and shade tolerant woody vines, are rare in the indigenous flora and, once introduced, find many niches to exploit (Lee, 1999; Williams, 1997).

### 1.3.2 Effects on indigenous biodiversity

Weeds have many effects on indigenous biodiversity, causing damage at the species, community and ecosystem levels. Weeds may also reduce genetic biodiversity, by hybridising with indigenous species (Reid, 1998).

Weeds increase the risk of extinction for already threatened species (Reid, 1998). Vegetation may be physically damaged by weed growth. For instance, vines such as old man's beard

(*Clematis vitalba*) may crush and break canopy plants after snow or rain (Williams, 1997). Weeds also compete with indigenous species for water, nutrients and other resources (Williams and West, 2000), including pollination and seed dispersal services (Reid, 1998). For example, wandering willie (*Tradescantia fluminenesis*) forms dense a ground cover and successfully competes for sites suitable for germination, thus inhibiting the regeneration of indigenous plants (Reid, 1998).

At the community level, weed invasion often results in decreased indigenous species richness (Batianoff and Franks, 1998) and changed structural characteristics of communities and ecosystems. Canopy stratification can be disrupted when weeds of a different growth form replace indigenous plants (Batianoff and Franks, 1998). Wilding pines (*Pinus* spp.), which invade tussock grassland in New Zealand, exemplify this effect (Williams, 1997).

Environmental weeds can also alter habitat by changing soil characteristics. For example, in New Zealand, exotic legumes such as tree lupin (*Lupinus arboreus*) add to available soil nitrogen (Reid, 1998), creating an environment more suitable for exotic species than those plants that evolved in infertile soils. Weeds may also influence geomorphology and hydrology (Williams and West, 2000). In several cases, plants have been deliberately introduced to improve land stability (Williams and West, 2000). Pampas grass (*Cortaderia* spp.) stabilises sand in dune systems, thereby changing the indigenous ecosystem and removing the habitat of some threatened plant species (Reid, 1998). The way in which a community is influenced by disturbance, such as fire or grazing, may be altered by environmental weed invasion (Williams, 1997). Gorse (*Ulex europeaus*) increases fire frequency by raising the abundance of combustible material, which has implications for indigenous species in gorse-invaded areas (Reid, 1998, Williams and West, 2000).

The relationship between weeds and biodiversity is not clear-cut; a range of disadvantageous and beneficial interactions between environmental weeds and New Zealand biota has been recorded (Reid, 1998). It is clear, however, that effective management of environmental weeds is an important element of biodiversity protection (Williams and West, 2000). Strategies for conservation management in New Zealand have recently been reviewed, which will have implications for environmental weed management and lowland forest protection.

## 1.4 Conservation in New Zealand

New Zealand signed the International Convention on Biological Diversity, ratified in 1993. The Convention requires signatory countries to take steps to prevent the loss of biological diversity at the genetic, species and ecosystem level, and to plan for the sustainable use of biological resources (DoC and MfE, 2000b). The protection of biological diversity is also required by national legislation (Jones et al., 1995).

It has been suggested that conservation in New Zealand needs to encompass the principle that biodiversity cannot be separated from the entire landscape (Craig et al., 2000; DoC and MfE, 2000). Conservation has traditionally focused on protection of charismatic endangered species and remote areas of great natural beauty, chiefly National Parks and Reserves (Clout and Saunders, 1995). Increasingly, commentators argue that conservation management in New Zealand needs to move from this narrow focus to address conservation of biodiversity in areas that are intensively used by humans (Craig et al., 2000; Norton and Miller, 2000).

One aspect of the re-focusing of conservation effort is to extend protection strategies to incorporate areas of indigenous habitat and vegetation on privately owned land (MfE, 2000b). This re-focusing is motivated by recognition that the conservation estate, although approximately 30% of the country's area, does not represent the full range of indigenous communities and ecosystems (Norton and Miller, 2000; DoC and MfE, 2000). Rather, protection is biased toward remote, mountainous areas (Awimbo and Norton, 1996). Lowland areas tend to be extensively cleared, leaving smaller habitat patches (Awimbo and Norton, 1996) that are typically highly modified by exotic plants and animals (Atkinson and Cameron, 1993; Clout and Lowe, 2001) yet support a disproportionate amount of national biodiversity (Ogden, 1995).

Another reason to extend conservation objectives relates to cross-boundary effects (MfE, 2000). Natural landforms, water courses, plants and animals do not recognise property boundaries, so it is necessary to manage whole landscapes in order to ensure the viability of remnant vegetation and habitat (Saunders et al., 1991). Legal protection does not of itself mitigate the threat of exotic animal and plant pests (Vila and Pujadas, 2001). Conservation, especially of lowland forest, needs to include on-going pest control and restoration of ecosystems that have been disrupted by pest species (Clout and Saunders, 1995; MfE, 2000). Burns et al. (in press) described remnants of kahikatea (*Dacrycarpus dacrydioides*) forest in a

matrix of pastoral land that has not been actively managed for conservation. The condition of the forest was poor: exotic species were present in all patches, and grazed, remnants had open, species-poor understories. The authors suggested that human activities at the landscape scale - chiefly flood control - have changed forest composition and will result in further loss by altering disturbance and recruitment patterns

It follows that conservation needs to address activities in the matrix, but management outside designated reserves is fraught with difficulties. Lowland forest conservation is a typical issue; protection and restoration of this habitat type is a necessary goal, but forest patches are vulnerable to invasive pests and other threats originating from the developed matrix and they are also often privately owned, which introduces another layer of complexity for the environmental manager.

### 1.4.1 Incentives for conservation

In spite of the general agreement that there is a valuable contribution to be made to national conservation by ensuring the sustainability of habitat outside the conservation estate, this will not be easily achieved (MfE, 2000b). Conserving indigenous biodiversity on private land involves balancing the benefits of conservation to the general public and costs to landholders, who lose the right to independent manage their property as well as potential financial losses (Davis and Cocklin, in press; MfE, 2000).

There is a strong feeling among rural landholders that, while conservation might be a virtuous goal, enforcement would create so much bad feeling as to be detrimental to achieving that goal (MfE, 2000b). Landholders' attitudes have considerable bearing on the effectiveness of conservation (Jones et al., 1995). An approach that stresses the importance of negotiating agreements with landowners, and encourages voluntary conservation by the provision of advice and incentives, is less likely to alienate landholders than strict regulation (MfE, 2000b). However it may be problematical in other ways.

The Resource Management Act 1991 (RMA) governs the management of indigenous biodiversity outside the conservation estate. It is intended to allow private development and ecosystem conservation to proceed in tandem (Norton and Miller, 2000) and has been praised for setting this goal (Craig et al., 2000). The RMA states that "the protection of areas of significant indigenous vegetation and significant habitats of indigenous fauna" is a matter of national importance which is to be "recognised and provided for" by "all persons exercising

powers and functions" under the Act (s6(c)). Those persons must also have particular regard to "the intrinsic values of ecosystems" (s7(d)).

The RMA has been criticised for devolving authority to the lowest possible level without ensuring that the bodies which assume responsibility for indigenous biodiversity have the power to ensure adequate conservation. This privileges development over conservation because it has an obvious economic value and, hence, political pull at the local government level (Davis and Cocklin, in press). The RMA does not clearly assign responsibility for the protection of indigenous vegetation to any organisation (Norton and Miller, 2000). Responsibility for protecting biodiversity outside the Crown estate has fallen to district councils, with mixed results. Councils are often unclear about their mandate with regard to nature conservation, especially on private land, and do not have the finance, information, or expertise to effectively manage biodiversity (Froude, 1997; MfE, 2000b). Councils define 'significant' at their discretion (Davis and Cocklin, in press), and assign different degrees of protection to indigenous vegetation (Davis and Cocklin, in press; Froude, 1997).

The Ministerial Advisory Committee on Biodiversity and Private Land was formed to investigate government options for fostering indigenous biodiversity on private land (MfE, 2000). The final report produced by the Ministerial Advisory Committee (MfE, 2000b) did not advocate direct intervention by national government, but stressed that decisions about regulation should continue to be made locally. It did, however, advise clarification of the responsibilities of local government and proposed that stronger direction should be provided by (a) amendments to the RMA, (b) non-statutory guidelines to support councils in meeting the requirements of the Act, and (c) establishment of a National Biodiversity Forum comprising representatives of all interest groups. It also advocated increased funding for councils, and the coordinated collection of information regarding the extent and quality of indigenous vegetation and habitat regionally and nationally (MfE, 2000b). These measures may address the failings identified by Froude (1997) and others, but have yet to be implemented.

The Committee also recommended increased effort in encouraging voluntary conservation. Proposed strategies include increased funding to non-government bodies like the Landcare Trust - which provides information and advice, as well as legal and financial assistance, to landholders - and encouraging the use of covenants and management agreements (MfE, 2000b).

One way to resolve conflict between private property rights and nature conservation is to apply incentives so that landholders are compensated for conservation costs, for instance by reduced rates or grants to assist with fencing costs (Jones et al., 1995). In parts of New Zealand, especially where pressure for subdivision in rural areas is intense, development rights can be exchanged for protection of indigenous habitat (Jones et al., 1995). Such a strategy has been operational in Rodney District since 1984 (Cocklin and Doorman, 1994), and has been adopted by at least seven other local authorities (Froude, 1997). That solution could raise more problems: subdivision and development introduce new threats including domestic animals and exotic plants, to forest remnants. The findings of this thesis, therefore, have implications for conservation management in the relatively densely settled lowlands of New Zealand.

## 1.5 The study area

Otatara is one of the most significant areas of indigenous vegetation in Invercargill City Council's jurisdiction (ICC, 2001). The peninsula is a fossilised sand dune system that was once covered by podocarp forest. Some remnants of that community remain, a rare example of *Podocarpus totara*, *Podocarpus hallii*[2] and matai (*Prumnopitys taxifolia*) forest on dunes, showing a pattern of forest composition related to dune age and structure (Norton, in press). Norton, who reviewed the state of indigenous forest at Otatara in 1996, suggested further development and fragmentation would increase the threat that environmental weeds pose to biodiversity in the area.

[2] It is not always possible to distinguish between these two species at Otatara (Matsui, 2000). The name 'totara' is used for both species throughout this thesis.

## 1.6 Research methods and thesis structure

There were three stages of research. The first was a literature review of published material regarding experimental and observational research into the process of weed invasion, and the factors that control the distribution of environmental weeds – discussed in Chapter 2. This review is used to generate several clusters of testable hypotheses regarding relationships between residential development in the matrix, other aspects of spatial context, conditions within the forest, and weed abundance. Chapter 3 sets the scene for data collection and analysis, summarise published sources to describe the environment at Otatara, and identifies groups involved in conservation.

The second stage of research consisted of the collection and analysis of observational data about weed abundance, spatial context and forest interior characteristics for 13 forest edge sites in Otatara. The methods used to collect and analyse data are described in Chapter 4, while Chapter 5 presents the results of analysis in terms of the hypotheses introduced in Chapter 2.

Finally, the results were interpreted in the light of the theory reviewed in earlier chapters to create a model that attempts to describe how plants spread into forest patches, and the ways by which residential development may facilitate that process. This model is presented and discussed in Chapter 7. The Conclusion, Chapter 8, suggests how the findings of this thesis could be used to guide forest conservation management at Otatara and elsewhere, and points to directions for future research.

# Chapter 2

# Weed Invasion and Residential Development

Environmental weed invasion threatens the viability of indigenous species and communities. Invasion is the process of a plant entering, establishing in, and spreading through an existing plant community. This review will hypothesise relationships between weed abundance, characteristics of forest habitat, and spatial context of forest. Testing of those will clarify how and to what extent weed invasion of nearby forest is enhanced by residential development.

A growing strand of ecological research considers how the spatial context of communities or habitats mediates ecological processes (Collinge, 2001; Swetnam et al., 1998). As noted earlier, weed invasion has a spatial element that has seldom been explicitly considered in research (Chapter 1). An aspect of spatial context that is important in fragmented landscapes - like Otatara - is land use in the matrix surrounding patches of indigenous habitat. This chapter first reviews some landscape scale studies of development, which often assume that residential development will cause deterioration of forest quality, in part, by facilitating weed invasion. However, there is only limited empirical data in support of this assumption.

The remainder of the chapter examines the argument that residential development increases the abundance of exotic plant species in habitat patches. It discusses the 'classic' weed invasion literature, which has identified several broad environmental controls of weed invasion, before returning to the specifics of residential development. The latter topic is explored through the literature discussing habitat fragmentation and ways in which changes to the spatial context of forest alter forest environmental conditions. Finally, it reviews the literature that directly discusses links between spatial context - particularly land uses in the matrix - and weed abundance in forest.

The primary purpose of this review is to derive testable hypotheses about relationships between spatial context, forest environmental conditions, and weed abundance. The over-arching aim is to find whether:

*Abundance of environmental weeds in forest patches is positively correlated with residential development in the matrix.*

## 2.1 Urbanisation and the quality of forest remnants.

Several studies have documented large-scale patterns of developed land and indigenous habitat. Authors often assume that residential development will inevitably cause forest quality to deteriorate. For instance, Medley et al. (1995) described forest landscapes on a gradient of urbanisation in a tract stretching 140 km northeast from New York City. With increasing proximity to the city, population density, traffic volume, road density and the prevalence of urban or residential land uses all increased, and forest patches became smaller and more numerous. The percentage of forest edges that bordered urban or residential land also increased but the paper does not explain how this last variable may be significant, except as one of several "important characteristics that influence [forest patch] ecology" (ibid. p166). In another example, Matlack (1997) described change since 1930 in forest distribution in the hinterland of a large city in the United States. In that period, forest cover increased considerably, as did urban and residential land uses. Over time, the distance between forest stands and the nearest house decreased, and the number of houses within 500m of forest increased (ibid). These trends were likely to associated with increased human disturbance of forest, particularly close to forest margins (section 2.5).

Norton (in press) documented changes to sand dune forest at Otatara as urbanisation increased between 1946 and 1996. The total area of forest and the number of remnants both declined. Remaining patches became, on average, larger and further apart. There were two phases of fragmentation: clearance for agriculture, resulting in reduction of forest area, was followed by clearance for residential development, which perforated the forest edges with small openings, a form of fragmentation that is becoming increasingly common near residential areas (ibid).

As well as such documentary studies, the theoretical effects of development have been simulated. For instance, Swetnam et al. (1998) constructed a Geographic Information System

(GIS) to model the effects of different arrangements of woodland patches and cultivated land in East Anglia on bird populations, for which there are detailed data regarding distribution and abundance. The authors claim their model can be applied to the management of any species or area "as long as ecological models exist to describe species distributions in relation to the landscape" (ibid. p4), leaving a gap to be filled by observational research and experimentation. Theobald et al. (1997) constructed a hypothetical model of the impact of different distribution and intensity of development, based on the assumption that the negative effects of housing projected from the cleared area into surrounding vegetation. Again, the model is not useful unless there can be confidence that the 'building effect distance' reflects the true extent of development impact, which can only be assessed from investigation of the real world.

Studies at the landscape level indicate how forest distribution changes with increasing urban and residential development, but should be linked with studies of the ecological outcomes of changes to landscape pattern (Collinge, 1996). There is a tendency to rely on generalisations drawn from landscape ecological theory or comparable research carried out in other locations, to draw conclusions about the probable outcomes of development. The work of Matlack (1997) is exceptional because its broad-scale observation was supplemented by field assessment.

There is no certainty that theory or results from research conducted in other regions, are a suitable basis for planning environmental weed management in the absence of local, empirical research (Woolley and Kirkpatrick, 1999). Invasion is a complicated and contingent process. The interaction of specific traits of a plant species and an invaded habitat together determine weed distribution. It has been suggested that, for this reason, research should focus on detailed single species analysis (Buist et al., 2000) or on very broad, macro-ecological, pattern analysis (Lawton, 1999).

Both techniques are problematic. Single species research requires significant time and resources, which may not be available to researchers given the large number of introduced species, each of which may become invasive (Lodge, 1993). In terms of generalisation, it is possible to make broad statements about factors that influence the probability of invasion, such as urban development and forest fragmentation, but such patterns cannot be taken for granted and should be supplemented by field observation or - ideally - controlled experiments to identify the mechanisms through which patterns emerge. The results can then be used to guide management.

## 2.2 Conditions that influence weed invasion

Controls on plant distribution operate at many levels. Yet, while there are generally accepted explanations for the natural distribution of plants at global or continental scales (Roy et al., 1999), understanding of contemporary change in plant distributions is poor. Lonsdale (1999) examined global patterns of exotic plant richness and found that indigenous species richness (a variable he terms a surrogate for area and habitat diversity), reserve status and island status explained most observed variation in weediness. The traits associated with higher numbers of exotic plant species were high indigenous diversity, non-reserve status (that is having no formal protection) and isolation (that is, being located on islands rather than continents).

There is also uncertainty about weed invasion of natural communities at the local scale, and why some communities appear to be more susceptible than others (Harrison et al., 2001; Hester and Hobbs, 1992; Prieur-Richard and Lavorel, 2000). Two conditions are necessary for any weed to successfully enter a new habitat. One is a suitable environment within the new habitat, that is, sites for exotic plant propagules to establish and thrive. The other is a source of propagules capable of dispersing into, and surviving within, the host community (Hobbs and Huenneke, 1992; Parendes and Jones, 2000). Attempts to explain weed invasion may refer to either the biology of weed species or to characteristics of the community entered (Burke and Grime, 1996; Cadenasso and Pickett, 2000; Crawley, 1987; Parendes and Jones, 2000). This chapter focuses on key characteristics of the habitat, rather than of the species (the biologies of the weed species considered here are outlined in Chapter 3).

An extensive literature discusses which environmental characteristics predispose host communities to weed invasion. Possible controls include diversity of the original community and competition within it, abiotic conditions of the original habitat, and disturbance - which modifies these other characteristics. Opportunities for dispersal - the movement of exotic propagules into an indigenous community - also control weed distribution.

### 2.2.1 Characteristics of the host community: competition and diversity

Competition for resources may limit opportunities for invasion. Invading species have to compete with the plants of the original community for the resources required for growth and reproduction: light, nutrients, water, and space (Naeem et al., 2000).

It is often argued that communities comprising many species are more resistant to weed invasion than those that are less diverse (Lodge, 1993; Levine, 2000; Naeem et al., 2000). Wiser et al. (1998) proposed two reasons for this, both of which hinge on resource availability. The first is that the area may not have been fully colonised and is capable of supporting more species than are currently present; if species are introduced they may be expected to establish readily. This second is that competition in species-poor areas may be less intense, so that exotic species can successfully out-compete locals. Variants of the theory have been proposed. For example: communities are likely to be more susceptible to invasion by exotic species from genera that are not represented in the original community (Rejmanek, 2000), or that exotic species are less likely to invade communities where many members of the same morphological guild as the invader are present (Wiser et al., 1998). In each of these arguments, competition is the driving factor; if the existing vegetation does not take full advantage of all resources, an exotic species of a new, or under-represented type, may exploit that gap in resource use (Prieur-Richard and Lavorel, 2000).

Theory is poorly supported by field observation (Levine, 2000; Naeem et al., 2000). Wiser et al. (1998) examined invasion of mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest by *Heiracium lepidulum*, an exotic perennial herb. Their findings yielded a positive relationship between indigenous species richness and presence of *Heiracium*. A positive relationship was also found between number of indigenous species of the same life-form as *Heiracium* and its presence. Other studies conducted at regional or larger scales have found that increased richness of indigenous species is positively related to increased richness of exotic species (Fensham and Cowie, 1998; Lonsdale, 1999). Lonsdale (1999) suggested that the greater habitat diversity of some areas has resulted in greater species richness (both exotic and indigenous). He distinguished that relationship, evident at regional scales, from the effects of competition intensity which, he suggested, might be significant at the local scale.

If competition from plants in the original community limits invasion, it might be expected that degradation of the vegetation will allow ingress of exotic species. Gilfedder and Kirkpatrick (1998) reported that exotic species cover is highest in remnants where the original vegetation has been degraded. This effect is not always apparent. Hester and Hobbs (1992) found that removal of native vegetation did not improve the growth of young exotic plants in recently burned shrubland in Western Australia.

Prieur-Richard and Lavorel (2000) found conflicting findings in their review of many observational and experimental studies that examined whether more diverse communities are less susceptible to invasion. They suggested that this was because confounding factors are

often unaccounted for. Other environmental characteristics may also determine community invasibility. Naeem et al. (2000) conducted an experiment with environmental characteristics held constant and found that theory was supported; performance of invasive species was inversely related to the diversity of host vegetation. More diverse communities appeared to be more competitive, in that resources necessary for growth were are scarce: plant biomass was higher, resulting in less available space above and below the ground, and levels of available light were lower (ibid).

However, competition is not necessarily strongest in sites with high species diversity. If a single plant species dominates a particular habitat and is efficient at using resources, then its abundance may be a strong control of the invasion process (Crawley et al., 1999, cited by Naeem et al., 2000). In addition to competition, other biotic features of the original community, such as herbivory (Hester and Hobbs, 1992), parasitism, or pathogens, may influence the establishment and spread of an exotic species (Burke and Grime, 1996; Prieur-Richard and Lavorel, 2000).

Levine (2000) examined a set of tussocks or 'islands' in a river system, each supporting a distinctive plant community. In the natural situation, incidence of three known environmental weeds was positively related to diversity of the host community but as the author noted, this could be due to covariance with another environmental factor. When diversity was artificially constrained and a known number of exotic seeds were introduced to each island, increased host diversity reduced the germination and growth of the introduced species, that is, the effects of diversity were evident at a small scale. Levine (2000) suggested that at broader scales other factors that covary with diversity exercise more control over invasion (section 2.2.5).

There is evidence that competition limits invasion when all other factors are constant, or at local scales, but the results cannot be extrapolated to situations where variation in other environmental conditions - such as light intensity or disturbance regime - can hide its effects (Naeem et al., 2000, Wiser et al., 1998). For this reason, the possible effects of diversity of the host community on the abundance of environmental weeds were not examined in this research.

## 2.2.2 Abiotic conditions: light, nutrients, and water supply

Plants have particular requirements for light, nutrients and water. A weed species will only establish in areas where its particular requirements are met. Overall, environments where these requirements are readily satisfied are more likely to be vulnerable to invasion. Larson et al. (2001) examined exotic plant abundance in an environment where water and nutrient availability limit plant growth. They found that mesic vegetation types tend to be more readily invaded than those of drier areas (ibid). Soil moisture is unlikely to be a limiting resource in Otatara, an area of relatively uniform topography and substrate and high annual rainfall.

Better-lit environments are also more vulnerable to invasion (Parendes and Jones, 2000). Naeem et al., (2000) in an experimental study of plant invasion of a prairie community, found that the growth performance of exotic plants was positively related to light availability. However, the light requirements of invasive species vary. Jesson et al. (2000) transplanted four known invasive species into a range of environments in the Arthur's Pass, New Zealand and found that one of the species survived best in plots with high light levels, while another preferred low light levels.

From those findings, it is hypothesised that light availability may in part explain the presence and abundance of environmental weeds at Otatara:

*1: Environmental weed abundance is positively correlated with light availability.*

It has been suggested that fertile soils are particularly susceptible to weed invasion (Burke and Grime, 1996). Soil fertility is defined as the ability of the soil to supply elements necessary for plant growth (Foth and Ellis, 1997) so it is not surprising that more fertile soils often support more weedy species. Several studies have reported a positive correlation between weed abundance and soil fertility. Wiser et al. (1998) found that mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest sites where *Heiracium*, an exotic herb, was present were significantly more fertile than those were it was not. In Australia, Fensham and Cowie (1998) noted that all major infestations of exotic species on two subtropical islands were in areas of nutrient-rich clay, and suggested that their distribution might be limited by low natural fertility elsewhere. Woolley and Kirkpatrick (1999) investigated the condition of forest remnants in lowland Tasmania and found that exotic species richness was greater where levels of phosphorus are high. Clements (1983) also noted that the abundance of weedy and

exotic species in northern Sydney bushland was positively related to phosphorus availability, which was increased by residential development.

That relationship has not always been demonstrated. A study of forest and scrub reserves in New Zealand found that soil fertility was not significantly associated with weediness, but the study was at a broad scale: fertility was classified as low, moderate or high for each reserve and analysis was conducted on data describing reserves throughout New Zealand (Timmins and Williams, 1991). Other research has found that relationships between soil nutrient status and the survival of weed species varies from species to species (Jesson et al., 2000). The relationship between soil fertility and weed abundance was tested at Otatara, against the hypothesis that:

2. *Environmental weed abundance is positively correlated with soil fertility.*

### 2.2.3 Disturbance

Enhanced disturbance of the host community is often correlated with intense weed invasion (Buist et al., 2000; Jesson et al., 2000; Harrison et al., 2001; Hobbs and Huenneke, 1992). For instance, Deferrari and Naiman (1994) studied the distribution of exotic plants in two forested catchments in Washington State and found that disturbance regime appeared to determine which areas are most heavily invaded. Exotic richness and abundance were highest on river bars, followed by - in decreasing order - clear-cut forest, older riparian areas, young forest, and mature forest. That sequence also represents increasing lengths of time since last disturbance for the set of habitat types.

Disturbance can be defined as a relatively discrete event driven by external factors that changes the survivorship of individuals or resource availability in an area (Hobbs and Huenneke, 1992). Disturbance encompasses a range of effects. Generally, it lifts the barriers to weed recruitment created by competition from the extant vegetation and abiotic factors such as available light or soil quality (Jesson et al., 2000; Prieur-Richard and Lavorel, 2000). For instance, disturbance may create a resource surplus, which exotic species are better suited to exploit than the original vegetation (Burke and Grime, 1996).

Disturbance may alter soil conditions, creating an environment favourable to exotic species. Changes to soil fertility, such as the addition of nutrients - like nitrogen and phosphorus - to nutrient poor soils may encourage the establishment of exotic plants (Hobbs and Huenneke, 1992). Addition of nutrients to low fertility soils has been shown to increase the presence and

dominance of exotic species in Australia (Clements, 1983). However, Hester and Hobbs (1992) found the increase in soil nutrients resulting from a fire in a western Australian reserve had no discernible effect on the abundance of exotic plants.

Mechanical soil disturbance aids weed establishment by temporarily increasing nutrient availability, reducing competition from neighbouring plants (Hobbs and Huenneke, 1992), and altering soil structure, which changes water infiltration rates and the moisture balance (Yates et al., 2000). Jesson et al. (2000) found that establishment of four environmental weeds from seed was successful only in plots where the soil was dug over, which they attributed to reduced competition. This conclusion is supported by the findings of Wilson and Tilman (1993), who have shown that intensity of competition (indicated by the difference between growth of target plants in plots where neighbouring plants remained *in situ* and control plots where neighbouring plants were cleared) is lower in disturbed environments.

Burke and Grime (1996) artificially created gradients of disturbance in a grassland community and found that percentage cover of introduced species is related to mechanical soil disturbance and fertiliser input, peaking when both are greatest. However, interaction of the two forms of disturbance also proved important; when soil disturbance was low, the effect of fertiliser addition was insignificant. Burke and Grime (1996) also showed the importance of competition from extant vegetation as a control on weed invasion. Exotic species establishment was most successful where the dominant indigenous species was damaged by disturbance (ibid.).

When a natural disturbance regime is altered, exotic species may prove better suited to the new regime than indigenous species. For instance, McCay (2000) suggested that establishment of sand pine (*Pinus clausa*) in a longleaf pine (*Pinus palustris*) community in Florida is related to suppression of natural fires and logging of mature trees. This disturbance resulted in conditions unsuitable for the germination of longleaf pine: viz lack of reproductive trees, a thick scrub understorey, and accumulated ground litter which does not hinder sand pine establishment. Frequent burning was found to be associated with decreased exotic species abundance in forest remnants in the humid lowlands of Tasmania (Woolley and Kirkpatrick, 1999). However, relationships between weed invasion and fire frequency are idiosyncratic. Dry forest remnants in Tasmania that were burnt in spring, at relatively short intervals, supported more exotic species than those burnt infrequently during winter (Gilfedder and Kirkpatrick, 1998).

Grazing is an example of ongoing disturbance with multiple, complex outcomes. It can facilitate weed invasion where exotic propagules are carried by farm animals, as well as by removing or damaging the existing vegetation, disrupting soil structure and adding nutrients (Hobbs and Huenneke, 1992; Prieur-Richard and Lavorel, 2000). It is generally accepted that grazing by agricultural stock significantly degrades temperate eucalypt forests by changing indigenous vegetation structure and composition and increasing exotic species abundance (Yates et al., 2000). Yates et al. (2000) found that grazed woodlands in the wheatbelt of Western Australia often had altered soil chemistry, compacted soil, reduced infiltration rates and increased evidence of erosion, and elevated levels of exotic species cover. Burns et al. (in press) reported similar results from New Zealand: heavily grazed kahikatea forest remnants had an unusually open understorey with many exotic species. Disturbance associated with feral animals has also been correlated with weed abundance (Fensham and Cowie, 1998).

The relationship is not universal, and grazing can control weed populations. Woolley and Kirkpatrick (1999) found that grazing reduced exotic species richness in forest remnants in lowland Tasmania because, they suggested, some exotic species are palatable to stock. In New Zealand, grazing damages *Amphibromus fluitans*, a threatened indigenous grass, but also suppresses the exotic species that may overwhelm it when stock are excluded (Reid, 1998).

Disturbance events may be natural, such as fire, or anthropogenic, such as the alteration of grazing regimes (Hobbs and Huenneke, 1992). The hypothesis tested at Otatara considers disturbance associated with residential development:

3. *Environmental weed abundance is positively correlated with intensity of anthropogenic disturbance.*

### 2.2.4 Summary: environment and weed invasion

Many environmental characteristics influence weed invasion and their interaction at a particular site creates a local context for invasion about which it is difficult to generalise (Burke and Grime, 1996). Although some relationships have been reported by many researchers, conclusions drawn from this review are probabilistic, they describe what is likely to happen, and should be verified with reference to the particular case of Otatara (Lodge, 1993). Hester and Hobbs' (1992) study of weed invasion in a Western Australian reserve illustrates this point. Their results show clear differences between two habitats: shrubland and open woodland. For instance, there were correlations between exotic plant abundance and

some measures of soil chemistry in shrubland, but not in woodland. In addition, the communities differed in their response to a common disturbance.

Interactions between characteristics of the host habitat and characteristics of an invading species control the success of invasion (Lodge, 1993). The Jesson et al. (2000) transplantation experiment illustrates the individuality of plant responses to variations in light regime, soil fertility and intensity of disturbance. Similarly, Burke and Grime (1996) found that different species have distinctive responses to particular combinations of disturbance.

Even though results from one study should not be extrapolated to all situations, some generalisations about environmental influences on weed invasion can be drawn. Competition from the original vegetation has a demonstrable effect on the success of invasion under experimental conditions, but this has rarely been observed in nature. Abiotic habitat characteristics are often related to environmental weed abundance, and disturbance significantly influences invasion success by altering the host habitat.

This discussion has focused on one necessary cause of weed invasion: presence of sites where weed establishment and growth are possible. Three factors likely to increase weed abundance were incorporated into testable hypotheses. The second necessary cause of invasion, dispersal opportunities, will now be discussed, before turning to the specifics residential development.

### 2.2.5 Dispersal

Successful invasion requires movement of plant propagules into a new area. Chances of invasion increase with increasing size of source populations of the invading species (Rejmanek, 2000) and a high influx of exotic propagules is often correlated with high rates of invasion (Harrison et al., 2001).

Many studies overlook dispersal by assuming that invasive plants can establish anywhere with favourable habitat conditions (Cadenasso and Pickett, 2000; Lonsdale, 1999). This is not necessarily the case, particularly in the early stages of invasion. For example, Wiser et al. (1998) found dispersal was an important control of *Heiracium* distribution in forest - its presence was strongly related to distance from the nearest pasture edge – in only the first year of their long-term study. Levine (2000) suggested that dispersal, rather than habitat conditions, explained the positive correlation between diversity and incidence of environmental weeds on his micro-islands; downstream islands supported more indigenous

species and were more heavily infested with environmental weeds. There was no causal relationship between host community diversity and weed establishment: when an equal number of exotic propagules were added to all islands there was no difference in establishment success. Levine (2000) proposed that location, representing dispersal opportunity, was responsible for the correlation: abundance of both exotic and indigenous species increased with distance downstream because downstream islands are exposed to a larger influx of propagules.

## 2.3 Forest fragmentation and the creation of edges

Much of landscape ecology is concerned with fragmented landscapes and the way in which the spatial context of a habitat patch mediates its condition (Collinge, 1996) and affects species distributions (Bolger et al., 1997). It provides a useful framework for examining the ways in which residential development may facilitate weed invasion. The role of landscape structure in weed invasion has not been a focus of research to date (Harrison et al., 2001; Parendes and Jones, 2000), often the characteristics of invaded habitat are examined in isolation from its spatial context, which may limit the applicability of research findings to management (Pickett and Cadenasso, 2000).

Hobbs (2000) argued that any landscape transformation creates opportunities for weed invasion in two ways: by changing the existing environment, providing opportunities for invasion, and by introducing new species to an area. Residential development has the potential to facilitate weed invasion by both mechanisms. The remainder of this chapter will discuss the mechanisms outlined in Chapter 1 in greater detail, beginning with an account of forest fragmentation.

### 2.3.1 Fragmentation

Fragmentation is the creation from previously continuous habitat of smaller, isolated habitat patches in a matrix of developed land (Collinge, 1996; Saunders et al. 1991). Otatara, like other New Zealand lowland areas, reflects clearance and fragmentation of previously extensive forest (Norton, 2000). Fragmentation alters the nature of the landscape in three ways. Firstly, some areas experience outright habitat clearance and establishment of new types of land cover. For instance, in New Zealand, a common change has been clearance of

lowland forest for exotic pasture grazed by introduced mammals (Norton and Miller, 2000). Secondly, the physical environment of the whole landscape is changed. In the wheatbelt region of Western Australia, fragmentation has altered the hydrologic cycle, causing greater runoff, flooding, and erosion due to reduced infiltration, rising water tables and reduced evapotranspiration (Hobbs, 1993). Clearance of indigenous vegetation and addition of artificial fertilisers to support exotic crops have also altered nutrient cycles (ibid). Thirdly, the remaining habitat patches are changed. They acquire new environmental attributes appropriate to their role as part of a fragmented landscape - size, shape, relative location, and age since fragmentation - which may influence the abundance of exotic plants within a patch (Gilfedder and Kirkpatrick, 1998).

It has been argued that the term 'fragmentation' should not be taken to mean creation of isolated remnants as well as reduction in extent of habitat cover, since these are separate phenomena with distinct effects (Bunnell, 1999). In particular, there is concern that some effects attributed to fragmentation result from habitat clearance, something that management which focuses on mitigating the effects of fragmentation may overlook. In many situations, such as Otatara, the two processes occur simultaneously.

The location of forest fragments determines regional biodiversity by 'sampling' once extensive habitat. Only a fraction of the original is preserved. Matlack (1997) noted that the locational bias of forest regeneration in Delaware, U.S. to lowland areas had increased the relative abundance of specialist species suited to those conditions. In New Zealand, concern has been expressed because most forest remnants are in upland and mountainous regions, as opposed to lowlands, although the latter account for a significant proportion of indigenous biodiversity (Ogden, 1995)

The size and relative isolation of a habitat fragment may influence weed invasion in two ways: loss of ecological integrity in the original community, and the increased importance of edges and edge-related environments (section 2.3.2). Loss of integrity occurs when indigenous species become rare or disappear and the altered communities become more susceptible to invasion. It is generally believed that the number of indigenous species supported in a habitat patch will decline following fragmentation: a process known as species relaxation (Saunders at al., 1991). Relaxation occurs when species do not have access to the environmental resources necessary to support viable populations within the reduced amount of habitat available to them. As well as species loss, other ecosystem processes within a habitat patch may be expected to change (Saunders et al., 1991).

Hobbs and Huenneke (1992) suggested that fragmentation could facilitate weed invasion by creating remnants too small to support 'natural' disturbance regimes and so be influenced by disturbance originating from within the matrix. It may also promote weed invasion by increasing the abundance of weedy, potentially invasive species in the cleared matrix and changing the character of remnant forest, particularly at edges (Brothers and Spingarn, 1992).

### 2.3.2 Edge effects

Fragmentation creates smaller, isolated and convoluted habitat patches that consist of relatively more edge than the original habitat. Edges are subject to characteristic effects, which extend into habitat patches from the surrounding developed land (Matlack and Litvaitis, 1999). Because of this, fragmentation results in habitat becoming dominated by the conditions of the external, developed, matrix (Saunders et al., 1991). Cadenasso and Pickett (2001) recently stressed the importance of researching the role of edges in weed invasion of forest remnants. A relationship between weed abundance and distance to the forest edge is often reported (Table 2.1), which suggests that weed abundance may be influenced by characteristics of the edge and adjacent land use (Boutin and Jobin, 1998).

Forest edges differ from the interior in terms of abiotic conditions, vegetation composition and structure. These differences are termed 'edge effects'. Physically, edges are more exposed to the effects of sun and wind, which create lighter, drier, windier conditions, hotter during the day and cooler at night than the forest interior (Matlack and Litvaitis, 1999; Saunders et al., 1991). Abiotic edge effects are unevenly distributed around forest patches. Young and Mitchell (1994) measured edge effects in several podocarp-broadleaf forest fragments in northern New Zealand and found gradients of air temperature and vapour pressure deficit from edge to interior. Gradients extended further from northern margins of fragments than from southern. They also found that abiotic edge conditions varied seasonally. The present research examines one climatic edge effect with implications for plant growth:

4. *Light availability is negatively correlated with distance from the forest edge.*

Soil fertility may also be different at patch edges because fertiliser applied to adjacent developed land can drift into the forest (Hester and Hobbs, 1992). Variation in the intensity of agricultural land use has been found to influence vegetation composition within adjacent habitat patches. A study carried out in Quebec reported that woodlot habitat adjacent to high intensity agricultural land supported greater numbers of short-lived, weedy and exotic species

than habitat adjacent to less intensively farmed land (Boutin and Jobin, 1998). This could result from fertiliser drift, herbicide drift, or other side-effects of agriculture (Boutin and Jobin, 1998). Hester and Hobbs (1992) reported a similar pattern at the interface between farmed land and shrubland, but this was not apparent at the edge of woodland which, they suggested, was because the open structure of woodland allows exchange of soil and fertiliser over larger distances so the pattern is not evident. The effect of fertiliser drift from developed land into forest was examined at Otatara:

5. *Soil fertility is negatively correlated with distance from the forest edge.*

In time, vegetation structure at the forest edge responds to the new physical environment. Generally, forest edges start with a well-developed canopy and sparse understorey vegetation but, eventually, trees bush out on the open side and a thick understorey develops (Matlack and Litvaitis, 1999). Edges may have greater density of small trees, saplings and shrubs than the forest interior (Harper and MacDonald, 2001). The time required for this 'wall' of vegetation to develop varies between forest types, and is influenced by land management in the matrix (Didham and Lawton, 1999). Edges do not inevitably close in this manner, and unravelling edges where edge conditions recede into interior forest have been noted in tropical forest adjacent to intensely cultivated land (Gascon et al., 2000). The physical structure of the forest edge controls the extent of edge effects. Didham and Lawton (1999) compared edges with and without dense regrowth in central Amazonia. They found that edge effects in air temperature, evaporative drying and ground litter characteristics extended farther into forest from more open edges.

It may be hypothesised that conditions within forest at Otatara are influenced by the structure of the edge:

6. *Increased closure of edge structure is negatively correlated with light availability.*

7. *Increased closure of edge structure is negatively correlated with soil fertility.*

### 2.3.3 Floristic change at forest edges

Biological responses to physical edge effects may alter forest structure and composition. An example of a direct structural change is greater exposure to the wind, leading to vegetation damage, so that the edge is sculpted by wind shear (Saunders et al., 1991).

Many edge effects are more complex, so it is difficult to precisely relate changes in abiotic conditions to changes in biota or to identify particular effects (Didham and Lawton, 1999; Murcia, 1995). Responses to edge formation may be indirect, mediated by a chain of ecological interactions (Murcia, 1995). However, some generalisations can be drawn with respect to vegetation composition, forest edges tend to support species that are uncommon in intact forest, including exotic species (Matlack and Litvaitis, 1999). Some forest species do not thrive in edge sites and become restricted to forest patch interiors (Matlack and Litvaitis, 1999; Young and Mitchell, 1994). For instance, with time, shade tolerant species become less common at edges (Saunders et al., 1991). In contrast, species suited to the edge environment - often those typical of disturbed environments, for instance with high light requirements - may become more common (Matlack and Litvaitis, 1999; Saunders et al., 1991). Some plant species appear to be indifferent to edge effects and do not show any trends in distribution with distance from the edge (Harper and MacDonald, 2001; Murcia, 1995).

Table 2.1 summarises several studies that report higher abundances of weed species at forest edges. Different techniques are used to quantify the distance decay effect, which - being a gradual change - is usually determined subjectively (Fraver, 1994). Other authors, although not quoting an 'edge-effect distance' as such, have noted that weedy and exotic species are most abundant at forest edges (Goldblum and Beatty, 1999; Matlack, 1994). The strength of this effect seems to vary with edge orientation, forest composition and structure and characteristics of the invasive species.

Buist et al., (2000) found no edge-related patterns in their study of a single environmental weed in urban bush land, but this may be because they defined edges by reference to roads and tracks, so gaps between patches were often narrow. It might also reflect the idiosyncratic responses of individual species to heterogeneous environments.

There are two potential explanations of an edge related distribution: that the environment of habitat edges favours the establishment and growth of invasive species, or that exotic species tend to enter habitat at edges and subsequent dispersal inward is slow. Documentary evidence supports both mechanisms.

**Table 2.1 Reported distances for raised abundance of exotic or weedy species at forest edges**

| Habitat | Measure | Distance | Author |
|---|---|---|---|
| Low, open forest dominated by *Banksia integrifolia* on sand dunes adjoining residential properties, coastal Queensland. | % of all species that are known weeds and number of known weed species | 500m | Batianoff and Franks (1998) |
| Hardwood forest, dominated by *Acer saccharum* and *Fagus grandifolia* adjoining cropland, central Indiana. | Number and frequency of alien species | Rapid decline to 8m, some species still present at 50m. | Brothers and Spingarn (1992) |
| Hardwood forest with *Acer saccharum, Fagus grandifolia* and others adjoining retired fields, Ontario. | % cover of all alien species<br>% cover of 18 environmental weeds | 10m<br>varies between species from 100m to 5m | Burke and Nol (1998) |
| Hardwood forest, dominated by *Quercus alba, Acer rubrum, Fagus grandifolia* and others adjoining agricultural land. | Relative cover of all exotic species | 10m (north facing), 60m (south facing) | Fraver (1994) |
| *Allocasuarina campestris* shrubland adjoining pasture, Western Australia. | % cover and number of exotic annual plants | 5m | Hester and Hobbs (1992) |
| *Acacia acuminata / Eucalyptus loxophleba* woodland adjoining pasture, Western Australia. | % cover and number of exotic annual plants | 50m (burnt), 85m (unburnt) | Hester and Hobbs (1992) |
| Bushland dominated by *Eucalyptus gummifera*, other eucaplypts and *Angophora costata* adjoining suburban development, Sydney. | % of all species that are exotic | Rapid decline to 30m (then slow change varying with development age - some species present 120m from old development) | Rose and Fairweather (1997) |

Woolley and Kirkpatrick (1999) found that exotic species richness and cover were higher at the edges of remnant forest in lowland Tasmania. They suggested that this could be due to either higher light levels at edges or less accumulated eucalypt litter, known to suppress many exotic species. Fraver (1994) reached a similar conclusion, because abundance of exotic species was found to be elevated much further into forest from south-facing than north-facing edges. He suggested this was because of climatic edge effects associated with incident solar radiation, which is stronger at south facing edges in the Northern hemisphere (Didham and Lawton, 1999).

The abundance of weeds at habitat edges may be because exotic plants enter habitat patches from the surrounding area (Cadenasso and Pickett, 2000; Harrison et al., 2001; Hester and Hobbs, 1992; Norton, 1996; Woolley and Kirkpatrick, 1999). That weeds invade indigenous habitat from edges is generally accepted in the New Zealand literature (Clout and Lowe, 2000; Owen, 1997; Reid, 1998).

Fragmentation increases the length of forest edge, which increases potential influx of exotic plant propagules from the exterior. In addition, increased turbulence at forest edges fascilitates movement of airborne material - including seeds - into the forest (Matlack and Litvaitis, 1999; Saunders et al., 1991). Sem and Enright (1995) found that the number of exotic species represented in the soil seed bank under kauri (*Agathis australis*) forest declined significantly with increasing distance from the nearest forest edge. Cadenasso and Pickett (2000) collected wind-dispersed seeds at forest edges in New York State and found the same pattern for seeds of non-forest species. In addition, larger numbers of seeds entered the forest, and seeds travelled further into the interior, where the edge was more open (ibid).

Bird dispersed seeds are often deposited at forest edges, which are commonly frequented by frugivorous birds because of the abundant perches, fruit and leaf cover they provide (Matlack and Litvaitis, 1999). Birds can also introduce seeds to the forest interior. Brothers and Spingarn (1992) found that wind dispersed exotic species were restricted to the exterior of forest patches while animal dispersed species were relatively more common in the interior. Williams and Karl (1996) showed that endemic and introduced bird species both dispersed the fruits of exotic plants into several small forest reserves in the South Island of New Zealand. Introduced birds ate larger quantities of exotic fruits. Species such as blackbird (*Turdus merula*) are the primary dispersers of many European plant species in their native range, and are common in urban areas - where weeds are likely to originate (see below) - and along indigenous forest edges (ibid).

Harrison et al. (2001) examined the distribution of two exotic grasses in a naturally patchy landscape. Serpentine soil does not normally favour exotic species, small areas of this soil and edges of larger areas were more likely to be invaded than their interiors. The proposed explanation was that "small patches and the edges of large patches might receive a high influx of alien propagules from the surrounding ... matrix" (Harrison et al., 2001 p46). The authors also examined a second hypothesis: that soils in sites close to patch edges were more like those of the matrix, a physical edge effect that might facilitate invasion, but found no supporting evidence.

It is therefore hypothesised that:

*8. Environmental weed abundance decreases with increasing distance from the forest edge.*

That being so, the size and shape of a habitat remnant could effect weed invasion. Small, or irregularly shaped patches will be more influenced by edge effects than those that are large or circular (Collinge, 1996; Saunders et al., 1991), It is expected that they will be more invaded. This was not evident in a study of Tasmanian bush remnants, where no significant relationship was found between exotic species diversity (or percentage cover) and patch size or shape (Gilfedder and Kirkpatrick, 1998).

Interactions across edges are contingent on the species and communities involved and the age of the edge (Pickett and Cadenasso, 1995). Young and Mitchell (1994) suggest that the abundance of mature individuals of some species, and the absence of juveniles, indicates that they were able to establish at the edge soon after patch creation, but not after that. Structurally, edges tend to 'close' with time and the influence of physical edge effects decreases (Didham and Lawton, 1999; Matlack and Litvaitis, 1999). Thus, it may become increasingly difficult for species originating in the matrix to enter the forest patch (Brothers and Spingarn, 1992). This permits the following hypothesis:

*9. Environmental weed abundance within forest is negatively correlated with increased closure of structure of the closest edge.*

Populations of exotic plants established at forest edges may, however, act as sources for the colonisation of suitable habitat, such as tree fall gaps, within the forest interior (Goldblum and Beatty, 1999).

## 2.4 The impact of development

Residential development is often associated with forest clearance and fragmentation, which is true of most changes in land use. For instance, in New Zealand, land transformation for pastoral farming has resulted in extensive forest clearance and fragmentation. The type of land use adjacent to the forest strongly influences the nature of the edge and the material that moves across it into the forest (Collinge, 1996; Gascon et al., 2000). For instance, Mesquita et al. (1999) found that land use in adjoining areas had significant influence on forest tree mortality, which has an edge-related distribution, in Amazonia.

Relatively few studies specifically examine the effects of residential development on weed abundance, but most report a positive correlation. Clements (1983) studied bushland in urban northern Sydney and found that bush patches surrounded by suburban development supported more exotic and adventive species than bush remote from development. Rose (1997) studied the same area, at a smaller scale, examining distribution patterns of *Pittosporum undulatum*. *P. undulatum* was more abundant along forest reserve edges than in the interior, and its abundance increased with increasing age of adjacent residential development. Overall exotic plant abundance showed a similar pattern, and sites closer to the developments of increasing age supported fewer indigenous species (Rose and Fairweather, 1997). A study of weed invasion of coastal vegetation on the Sunshine Coast, Queensland also found that diversity of weed species decreased with increasing distance from residential dwellings (Batianoff and Franks, 1998).

At a coarser scale, Fensham and Cowie (1998) found numerous exotic species naturalised in and around settlements on two islands in the Northern Territory of Australia, while few had naturalised in undeveloped areas. A study of wetland plants in Portland, Oregon, found that wetlands bounded by agricultural, commercial or industrial landuses, or by transport corridors, supported more exotic species than wetlands bounded by undeveloped land (magee et al., 1999). Intrinsic habitat characteristics, particularly the moisture regime, were also significant controls of floristic composition (ibid).

Regional comparison of areas along the coast of Queensland showed a greater proportion of the total flora is exotic in more densely populated regions (Batianoff and Franks, 1998). Similarly, Roy et al. (1999) found a positive relationship between exotic species richness and urban landcover in Great Britain. Crawley (1987) made a similar comparison using published

county floras and noted that habitats close to or within cities supported more exotic plants than those that were remote from development. The number of exotic plant species was positively correlated with human population of subtropical Australian islands (Fensham and Cowie, 1998) and the same relationship was found, at a very large scale, for states of North America (McKinney, 2001). Similarly, Vila and Pujadas (2001) found positive relationships between the density of alien plants and indicators of development - the human development index, value of imports, and length of transportation networks, and percentage of land protected for conservation - for 28 countries in Europe and North Africa.

Care is needed in extrapolating findings from large-scale studies to the New Zealand situation, because they often consider the total exotic flora rather than environmental weeds. Further, they often do not distinguish between the effect of habitat loss associated with urbanisation and other effects. Thus, Roy et al. (1999) concluded that although exotic species diversity is likely to increase as an area becomes more urbanised, indigenous plants may persist if existing woodland is preserved. An aim of this study is to ascertain if this assumption is valid for Otatara.

Timmins and Williams (1991) attempted to explain weed abundance in New Zealand forest and scrub reserves with reference to 15 characteristics of reserves, ranging from the diversity of the indigenous plant community to intensity of recreational use, and including surrounding landuse. Distance from the reserve to the nearest town with greater than 5 000 inhabitants showed the strongest correlation with weed diversity in a reserve (ibid).

Most researchers seem to have followed the coarse-scale research approach advocated by Lawton (1999), and examined broad patterns of weed distribution, avoiding the contingency that blurs patterns at the local scale. Few researchers examined the mechanisms by which urbanisation and increased population density enhance weed abundance. The following sections discuss those mechanisms. As well as fragmentation and habitat clearance, there is evidence to suggest that residential development increases weediness through enhanced propagule supply and dispersal opportunities, and by increased disturbance creating conditions suitable for weed establishment.

## 2.5 Residential areas as a source of propagules

As discussed earlier, weed invasion is related to high rates of influx of exotic propagules and, hence, to increasing size of the source populations (Rejmanek, 2000). Similarly, it is related to the diversity of the pool of potential invaders. This is a common ecological pattern: the larger the regional pool of species, the greater the species richness of any site (Lawton, 1999).

Humans have long been involved in plant dispersal (Mack and Lonsdale, 2001; Hodkinson and Thompson, 1997) with many species transported internationally for agriculture or horticulture (Prieur-Richard and Lavorel, 2000). Mack and Lonsdale (2001) identify three phases of plant introduction in European colonies. Initially, colonists inadvertently introduced adventive species to new areas. Secondly, plants with utilitarian value were deliberately introduced. And thirdly, there was the introduction of species with aesthetic value, either as reminders of 'home' or as exotic specimens. Mack and Lonsdale (2001) suggest that the 'aesthetic' phase now prevails, greatly expanding the amount and diversity of international introductions.

Humans also facilitate dispersal at smaller scales (Mack and Lonsdale, 2001). Wholesale and retail nurseries are very effective at disseminating exotic plants across whole countries (Hayden Reichard and White, 2001). At the local scale, as previously discussed, rates of influx into forest may be increased by development and fragmentation creating relatively longer edges. Rose (1997) found that the age structure of P. undulatum at edges abutting residential development suggested that the species invades forest by spreading progressively inward.

Residential development may increase the rate of invasion by increasing the number and diversity of exotic propagules on land adjacent to forest. Gilfedder and Kirkpatrick (1998) found that exotic species richness was significantly higher in forest patches surrounded by suburban gardens than farmland. They suggested that this was because suburban forest remnants are exposed first to agricultural weeds and, after development in the matrix, to garden escapes; in total, a much wider range of invasive species. Gardeners often deliberately introduce exotic, aesthetically pleasing plants (Mack and Lonsdale, 2001). Some of those subsequently 'escape' from cultivation and become environmental weeds (Batianoff and Franks, 1998; Cronk and Fuller, 1995). In fact, Brothers and Spingarn (1992) found evidence that garden escapes tend to be more successful invaders of forest than agricultural weeds.

An example of a popular garden species that has escaped from cultivation in New Zealand is aluminium plant, *Galeobdolon luteum* (Roy et al., 1998). Gardeners may even cultivate species after they have been registered as environmental weeds (Hayden Reichard and White, 2001).

Weeds that are not intentionally cultivated also derive from gardens. A study of human-mediated plant dispersal in Sheffield found many weedy species in commercially marketed topsoil, and in potted plants sold by garden centers and nurseries (Hodkinson and Thompson, 1997). Batianoff and Franks (1998) noted that exotic species were most abundant in those parts of their coastal study area that had been reclaimed or top-dressed with soil from elsewhere, but this effect might also be because of the added soil nutrients.

Timmins and Williams (1991) suggested that their results reflect the role of a town as the origin of many weed species. In the Auckland region, for instance, some exotic species only occurred within 1 km of a major town (Timmins and Williams, 1991). As well as distance to the nearest town, several of the characteristics related to weed abundance in reserves were associated with human activities: rubbish dumping, increased proximity to road or rail corridors, and increased intensity of recreation (Timmins and Williams, 1991). Two of those factors disperse weed propagules. Road and rail corridors are disturbed areas, which support weedy species and operate as dispersal corridors across landscapes, while rubbish dumping is more likely to be evident at the small scale, in Otatara.

### 2.5.1 Road and rail corridors

Road corridors are often associated with high levels of exotic species richness and cover (Lugo and Gucinski, 2000; Parendes and Jones, 2000). They aid weed invasion by providing highly disturbed habitat suitable for weed establishment and offer dispersal opportunities (Parendes and Jones, 2000).

Many types of disturbance are associated with roads, including grading of unsealed roads, vegetation cutting, and ditch clearing (Parendes and Jones, 2000). These activities tend to favour the establishment of adventive species, which may then spread from the disturbed corridor into indigenous habitat (Lugo and Gucinski, 2000). Parendes and Jones (2000) examined the distribution of exotic species along frequently used roads, rarely used roads, abandoned roads, and streams in extensive forest in Oregon. Exotics were most abundant

near busy roads, presumably because light levels were higher; disturbance had changed habitat conditions and enabled weed establishment.

Roadsides seem to be stepping-stones to further invasion. Exotic species were usually absent from canopy gaps distant from roads, but present in clear-cuts close to roads (Parendes and Jones, 2000). Road and rail corridors are known to act as conduits for exotic plants (Lugo and Gucinski, 2000). Seeds may be carried deliberately in cargoes, or fortuitously as debris attached to vehicles (Hodkinson and Thompson, 1997). Transit corridors may also enhance windborne transport (Hodkinson and Thompson, 1997) and improve human access to forest remnants;, which increases disturbance and propagule dispersal associated with recreation (Matlack, 1993; Timmins and Williams, 1991).

### 2.5.2 Rubbish dumping

Dumping of garden waste is an effective mode of weed dispersal, combining propagule introduction with environmental disturbance; dumps are also likely to show enhanced soil fertility (Batianoff and Franks, 1998). Matlack (1993) surveyed 40 suburban forest remnants in Delaware and reported a wide range of garden rubbish in forest interiors, including lawn clippings, leaf piles, pruned limbs, and inorganic rubbish.

Of the 193 species identified in the *Botanical Society of the British Isles Monitoring Scheme* as increasing in range throughout Britain, 37% are known garden escapes (Hodkinson and Thompson, 1997). Disposal of garden plants is a probable means of 'escape'. Hodkinson and Thompson (1997) questioned gardeners about their habits of plant disposal. The most commonly reported strategies are unlikely to result in that problem, but dumping was also reported. Species that gardeners disposed of were typically tall, spreading perennials with a tendency to vegetative reproduction, all characteristics of known garden escapes. The main reason given for disposal was that plants were spreading aggressively within gardens, suggesting they are also likely to persist in the wild (Hodkinson and Thompson, 1997). In New Zealand, some species, such as yellow wild ginger (*Hedychium flavescens*) and wandering willie (*Tradescantia fluminensis*) - which spread vegetatively - are dispersed almost entirely by dumping (Timmins and Williams, 1991).

Considering the potential role of gardens as a propagule source at Otatara, it is hypothesised that:

*10. The number of environmental weed species in the matrix is correlated with residential development.*

*11. The abundance of environmental weed species within forest is correlated to number of weed species in the nearby matrix.*

## 2.6 Disturbance associated with residential areas.

Plants common in urban areas are not distinguished by being suited for dispersal on humans or vehicles (Roy et al., 1999). Rather, they tend to be tolerant of intense habitat disturbance (ibid), suggesting that factors other than improved dispersal opportunities may explain high weed abundance in the hinterland of urban areas. Development may facilitate weed invasion because it changes environmental conditions within nearby indigenous habitat. Rose and Fairweather (1997) found that the species (often exotic) that became more frequent in forest near residential development are characteristic of nutrient rich, wetter environments, while forest remote from development was dominated by species adapted to low nutrient conditions and regular burning.

Fensham and Cowie (1998) suggested that artificially increased soil fertility in developed areas might in part explain the correspondence they observed between presence of urban settlements and diversity of naturalised exotic plants. Similarly, King and Buckney (2000) noted that streams in urban areas supported a distinctive aquatic flora (mostly exotic) that favoured high nutrient concentrations, and had high nutrient concentrations relative to those in undeveloped catchments. It can be hypothesised that:

*12. Soil fertility is correlated with residential development.*

Forest patches in residential areas are often subject to high levels of human disturbance through activities like path or camp clearing, trampling, plant collection, and fire wood gathering (Friesen, 1998; Matlack, 1993). Matlack (1993) termed such disturbance "sociological edge effects" because it is concentrated at forest borders and its effect declines with distance into the forest. Matlack (1997) found that human related disturbance was (a)

most intense close to the forest edge and (b) related to residential development: degree of disturbance increased as distance to the nearest house decreased. This suggests two effects that the spatial context of forest at Otatara might have on anthropogenic disturbance:

*13. Intensity of anthropogenic disturbance is positively correlated with residential development.*

*14. Intensity of anthropogenic disturbance is negatively correlated with distance from the forest edge*

Anthropogenic disturbance can lead to changes in vegetation composition. Hoehne's (1981) comparative study of forest patches in Milwaukee showed that several indigenous herbs had declined in abundance over 24 years of increased urbanisation while some exotic species had become more common. Species richness was related to degree of disturbance, with disturbed sites having greater diversity, perhaps because there were more weedy and exotic species in disturbed sites (ibid). Rose (1997) also considered links between residential development, disturbance, and weed invasion. He evaluated anthropogenic disturbance in his study of the distribution of *P. undulatum* and found that it was most intense at the bush edge and seemed to increase with age of adjacent development. Abundance of *P. undulatum* was significantly correlated with degree of anthropogenic disturbance.

This correlation is not always apparent. Larson et al. (2001) found that diversity and abundance of exotic plants were not appreciably higher in prairie grassland classed as disturbed: that is, within 100m of a modified area such as roads, tracks, campsites, or areas planted with exotic species. Instead, vegetation type - representing intrinsic characteristics of the site - was the most significant control of weediness. This result is surprising, considering that the researchers' definition of disturbed areas encompassed the role of roads, campsites and such like as sources of weed propagules.

Like general disturbance, anthropogenic disturbance encompasses a range of impacts. For instance, rubbish dumping, which has been discussed above, is a form of anthropogenic disturbance (Matlack, 1993). Two other types of anthropogenic disturbance pertinent to residential development are discussed in more detail below.

## 2.6.1 Recreation

Lonsdale (1999) reported that exotic species richness in environmental reserves on two continents increased with increasing visitor numbers even when the potentially confounding effects of reserve size were accounted for. He suggested that this could be attributed to two aspects of recreation: that visitors increased the amount of disturbance, creating sites for establishment and growth, and that visitors were vectors for the dispersal of exotic propagules.

Recreation enables weed establishment by creating opportunities for growth via soil disruption, removal of organic litter, and damage to extant species (Matlack, 1997). The creation of walking paths and unofficial tracks was found by Bhuju and Ohsawa (1998) to result in soil compaction and slightly reduced levels of carbon and nitrogen in the soil, which they suggested were due to reduced accumulation of plant litter. Walking also reduced herbaceous cover and changed vegetation composition and structure. Some species were found exclusively in trampled sites (ibid). Kuss and Hall (1991), in an experimental study of the effects of trampling on forest vegetation, found similar results: trampled sites had more compacted soil, lower species diversity and decreased overall plant cover. These changes were evident even in sites exposed to low intensity trampling (ibid).

Suppression of the original vegetation provides opportunities for invasive species. Jesson et al. (2000) compared growth from seed and cuttings of four weed species in South Island forest for plots (a) close to a tramping track (b) in undisturbed vegetation, and (c) manually disturbed areas. Artificially disturbed areas showed the highest germination and growth rates, although only one species did significantly better in plots close to tramping tracks.

Human traffic can enable plant dispersal into habitat remnants because seeds are carried on clothing and footwear (Hodkinson and Thompson, 1997). Further, Matlack (1993) found that various forms of anthropogenic disturbance, including rubbish dumps, were clustered around walking tracks - another reason why dispersal is enhanced in recreational zones.

## 2.6.2 Management

Some human activities carried out in or adjacent to natural habitat can be seen as management, but may be detrimental to indigenous biodiversity. For instance, logging of indigenous forest can encourage exotic species (Woolley and Kirkpatrick, 1999) and

hydrological conditions are altered by artificial drains (Norton, 1996) to the of benefit exotic species. However, some activities, such as removal of weeds within forest, are undertaken deliberately to improve the quality of habitat in suburban areas (Norton, 1996). A very wide range of potential management activities may take place in forest at Otatara, and the effects of these are examined generally in terms of the hypotheses involving disturbance discussed above, and in terms of changes to edge structure.

Management activities such as tree planting on land adjacent to forest patches can seal the edge and reduce edge effects (Norton, 2000). However, it may be expected that increased traffic into the forest will maintain an open edge structure, and that disturbance will be high where this is the case. Thus, two more hypotheses are proposed:

15. *Increased closure of edge structure is negatively correlated with residential development.*

16. *Edge structure is correlated with anthropogenic disturbance within forest.*

## 2.7 Conclusion

Some landscape level studies of urbanisation and forest fragmentation have assumed that the juxtaposition of forest and residential areas will result in degradation of indigenous forest, including enhanced weed invasion. Such broad scale, descriptive studies should be supplemented by local field observation or experimentation. The purpose of this thesis is to evaluate the extent to which Norton's (in press) proposals about remnant forest at Otatara are supported by field observation.

Two things are necessary for successful plant invasion of indigenous habitat: effective dispersal of invasive plant propagules, and the existence of suitable sites for establishment. The literature reviewed in this chapter has suggested a number of potential mechanisms by which residential development can alter these necessary conditions for weed establishment.

A number of testable hypotheses have been developed in the course of this review. The overall research hypothesis is that:

*Abundance of environmental weeds in forest patches is positively correlated with residential development in the matrix.*

The others are grouped below. Several of these have been assessed before, in a range of locations, but are relevant to Otatara because they underlie the theorised mechanisms that are the subject of this research.

The first hypotheses concern correlations between environmental weed abundance and habitat conditions:

1. *Environmental weed abundance is positively correlated with light availability.*

2. *Environmental weed abundance is positively correlated with concentrations of soil nutrient.*

3. *Environmental weed abundance is positively correlated with intensity of anthropogenic disturbance.*

Hypotheses 4-8 deal with edge effects, involving habitat conditions and environmental weed abundance, which have been widely documented and Hypothesis 9 follows from these ideas:

4. *Light availability is negatively correlated with distance from the forest edge.*

5. *Soil fertility is negatively correlated with distance from the forest edge.*

6. *Light availability is negatively correlated with increased closure of edge structure.*

7. *Soil fertility is negatively correlated with increased closure of edge structure.*

8. *Weed abundance decreases with increasing distance from the forest edge.*

9. *Environmental weed abundance is negatively correlated with increased closure of edge structure.*

The final seven hypotheses directly concern how residential development in the matrix can change the forest environment and promote weed invasion.

10. *Number of weed species in the matrix is correlated with residential development.*

11. *The abundance of environmental weed species within forest is correlated to number of weed species in the nearby matrix.*

12. *Soil fertility is correlated with residential development.*

13. *Intensity of anthropogenic disturbance is positively correlated with residential development.*

14. *Intensity of anthropogenic disturbance is negatively correlated with distance from the forest edge*

15. *Increased closure of edge structure is negatively correlated with residential development.*

16. *Edge structure is correlated with anthropogenic disturbance within forest.*

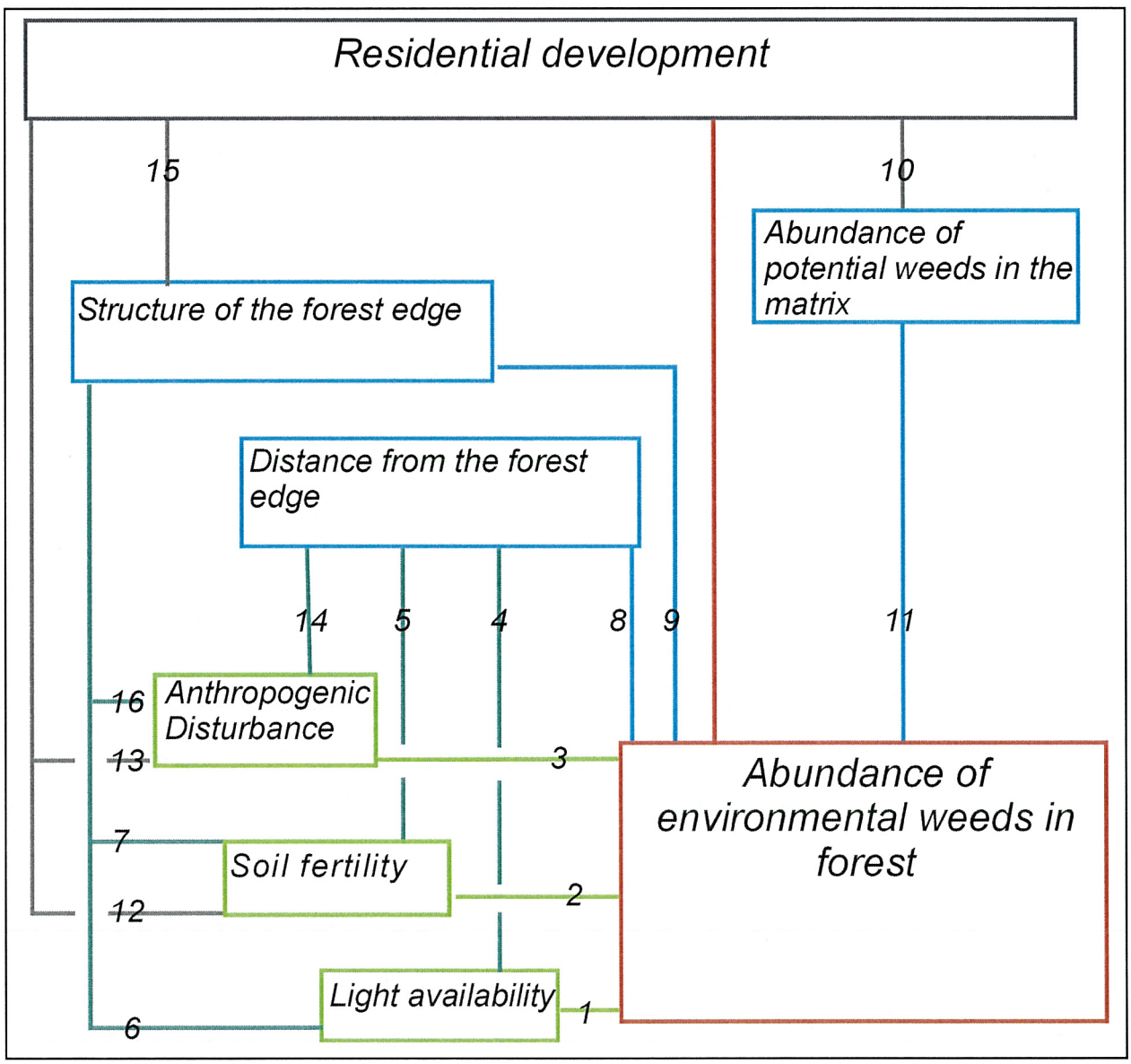


**Figure 2.1 Hypothesised correlations between residential development, other aspects of spatial context, forest interior characteristics and weed abundance.**

All 16 hypotheses concern specific, and related, aspects of this research (Figure 2.1). The overarching research hypothesis is shown in red. The four links shown in black relate residential development to other environmental factors that may influence weed abundance. Two (Hypotheses 10 and 15) describe the effect residential development is likely to have on other relevant aspects of the spatial context of forest. Two describe effects that residential development may have on conditions within the forest (12 and 13). Links shown in sea-green concern correlations between spatial context and characteristics of the forest interior (Hypotheses 4, 5, 6, 7, 14, and 15). The three links shown in blue represent correlations between weed abundance and aspects of spatial context (8, 9 and 11), and those in green concern correlations between weed abundance and forest characteristics (1, 2 and 3).

Investigation of the hypotheses requires quantification of each boxed element shown in Figure 2.1. This list of factors does not include all potential controls of weed distribution, but it is sufficient to show whether or not there are links between residential development and weed invasion of nearby forest patches.

Data describing each element was obtained from Otatara. The following chapter will introduce the field area, highlighting the characteristics that make it suitable for this research. Later chapters will describe the results of data collection and analysis and relate these to the theory reviewed in this chapter, leading to a conceptual model relating weed invasion and residential development.

# Chapter 3

# Setting the Scene

Colonisation remodelled the New Zealand landscape. Habitat clearance and fragmentation, along with introduced species, have depleted indigenous biodiversity and threaten remaining species and habitat. Residential development is a significant cause of ongoing habitat fragmentation and may exacerbate weed invasion.

This chapter starts by describing national environmental weed management strategies, before turning to the local case of Otatara and its weed species. Otatara is suitable for this research because it contains both residential development of different ages, and indigenous vegetation threatened by weed invasion. The physical environment and history of forest modification of Otatara are discussed. Local conservation strategies are also outlined, to indicate the conservation values of the area and measures taken to preserve these values.

Finally, this chapter introduces the 21 environmental weeds targeted in this research (Table 3.1). The limited success of attempts to identify plants with weed potential by considering their biological characteristics is discussed. Nonetheless, the biology of a weed contributes to an explanation of its distribution (Williams, 1997) and is relevant to this study.

## 3.1. Weed management in New Zealand

Two influences have shaped the biota of New Zealand since colonisation: destruction and fragmentation of indigenous habitat, and introduction of exotic plant and animal species (Craig et al., 2000). Those processes created the current situation, wherein invasive species threaten the viability of indigenous biodiversity (Atkinson and Cameron, 1993; Clout and Lowe, 2000; DoC and MfE, 2000; Reid, 1998).

New Zealand was almost entirely forested in the recent past (DoC and MfE, 2000). Clearance began after initial Polynesian colonization and is established by radiocarbon dating of presumed anthropogenic charcoal in the South Island at approximately AD 1250 (Ogden et al., 1998). The date is debated, but recent estimates of initial anthropogenic clearance in the North Island, based on tephrochronology, yield a similar range: AD 1280 - 1400 (Lowe et al., 2001). More land was cleared after European colonization began, and approximately a third of New Zealand is now covered by indigenous vegetation (DoC and MfE, 2000b).

The remaining forest is mostly in the southwest South Island (Clout and Lowe, 2000). Steep, high altitude areas are likely to be covered with indigenous vegetation, while lowland, coastal areas tend to be denuded, with highly modified forest remnants, as Awimbo and Norton (1996) demonstrated for the Hokitika Ecological District. The conservation estate shows similar bias: lowland reserves are small and isolated (Ogden, 1995), most lowland forest is privately owned (MfE, 2000b). Intensive forest fragmentation and development in lowland coastal areas have increased the vulnerability of remnant forest to invasive species. Clearance has created primarily open lowland habitats, which favour exotic species that spread into habitat remnants (Clout and Lowe, 2000).

Environmental weeds are particularly deleterious where indigenous habitat is highly fragmented and modified by development (Owen, 1997). Human activity introduces exotic propagules and alters disturbance regimes, successional patterns, and other habitat characteristics (Reid, 1998). Development is most intensive in the lowlands, increasing the risk to remaining forest (MfE, 2000b). Despite this, those forests support a large amount of biological diversity (Ogden, 1995). Their protection is a national conservation priority (DoC and MfE, 2000).

### 3.1.1 Management at a national level

Several government bodies are involved in managing environmental weeds. New introductions are managed by the Environmental Risk Management Authority, which considers all proposed introductions, and the Ministry of Agriculture and Forestry, which polices accidental or illicit introductions (Williams and West, 2000). The Department of Conservation (DoC) may consult those bodies regarding plants likely to threaten indigenous biodiversity (Owen, 1998). Weeds already in New Zealand are managed under the

Biosecurity Act 1993, the Conservation Act 1987, and the Resource Management Act 1991 (RMA).

The Biosecurity Act 1993 seeks to control known weeds largely through Pest Management Strategies (PMS) created and administered by Regional Councils (Owen, 1998). DoC may be involved in that process, and can create National Pest Management Strategies in some circumstances (Owen, 1998). For a pest to be managed under a PMS, the benefits of control must outweigh the costs (Owen, 1998), which is difficult to prove in respect of biodiversity. Thus the Act focuses on management of agricultural weeds, with limited attention to environmental weeds, especially newly established or potential pests (DoC and MfE, 2000). A complicating factor is that Regional Councils may not have sufficient skills or capital to undertake this type of management (DoC and MfE, 2000). Commentators advocate the Act be revised to facilitate biodiversity protection (MfE, 2000b).

The Conservation Act 1987 established DoC. Along with legislation like the Reserves Act 1977, it requires DoC to protect the Crown Conservation Estate from environmental weeds (Owen, 1998). Because weeds spread into reserves from elsewhere, DoC plays a role in weed control on private land either directly, with the landholder's agreement, or through advocacy and information sharing (ibid).

DoC promotes two strategies for environmental weed control. One is control of key species, usually those new to a conservancy (DoC administrative units); the other is targeted elimination of all weeds from areas of high conservation value (Owen, 1998). The intention is to direct control where it will be most effective. However, the principle of targeted protection of key areas has been criticised for fear it will lead to improvement in the quality of few areas while the bulk of the conservation estate becomes degraded (Craig et al., 2000).

The RMA governs treatment of indigenous vegetation and habitat on private land (MfE, 2000b). As noted earlier (Chapter 1), it has had mixed success. Responsibility for protecting biodiversity is devolved to local councils, and there is considerable variation in the degree of protection assigned to indigenous vegetation (Davis and Cocklin, in press; Froude, 1997). Councils are often unclear about their responsibilities with regard to nature conservation and may not have the finances, information, or expertise to undertake effective conservation (Froude, 1997; MfE, 2000b). The Ministerial Advisory Committee on Biodiversity and Private Land was formed to address those issues (Chapter 1) but its recommendations have

yet to be implemented. At Otatara, the where fieldwork was done for this research, conservation is managed locally.

## 3.2. The study area: Otatara, Southland

Otatara is several kilometers west of Invercargill, the largest city in Southland (Figure 3.1). Otatara contains a rare example of podocarp forest on a fossil sand plain (Norton, in press), but has been partly cleared for agriculture in the past and forest remnants are under pressure from continuing residential development (DoC, 1998).

### 3.2.1 The physical environment

The climate of coastal Southland is dominated by strong westerlies (SRC, 1997), but northerly winds are common. The windiest period at Otatara is between September and January, and around the autumn equinox (ICC, 2000). The mean annual rainfall of 1042mm is evenly distributed throughout the year; on average, 156 days have rainfall of 1mm or greater (ICC, 2000). Mean annual air temperature is 9.7°C. The warmest months are January and February, with mean temperatures of 14°C, and the coolest is July (4.5°C). Invercargill experiences, on average, 111 days of frost per year (ICC, 2000). The sky is often overcast, with sunshine only 42 % of the possible time in winter and 35 % in summer (Norton, in press).

Geologically, the peninsula is composed of Otatara gravels (ICC, 2000) overlain by stabilised sand dunes and plains, less than 6 000 years old (Norton, in press). Soils are Otatara yellow-brown sands, which developed under forest (DSIR, 1968). These are typically of low fertility, but suitable for pasture. Nitrate availability, represented by the C:N ration, is medium, in the upper soil layers. Base cation concentrations are low, except where shells provide calcium, and phosphate availability is also low (DSIR, 1968).

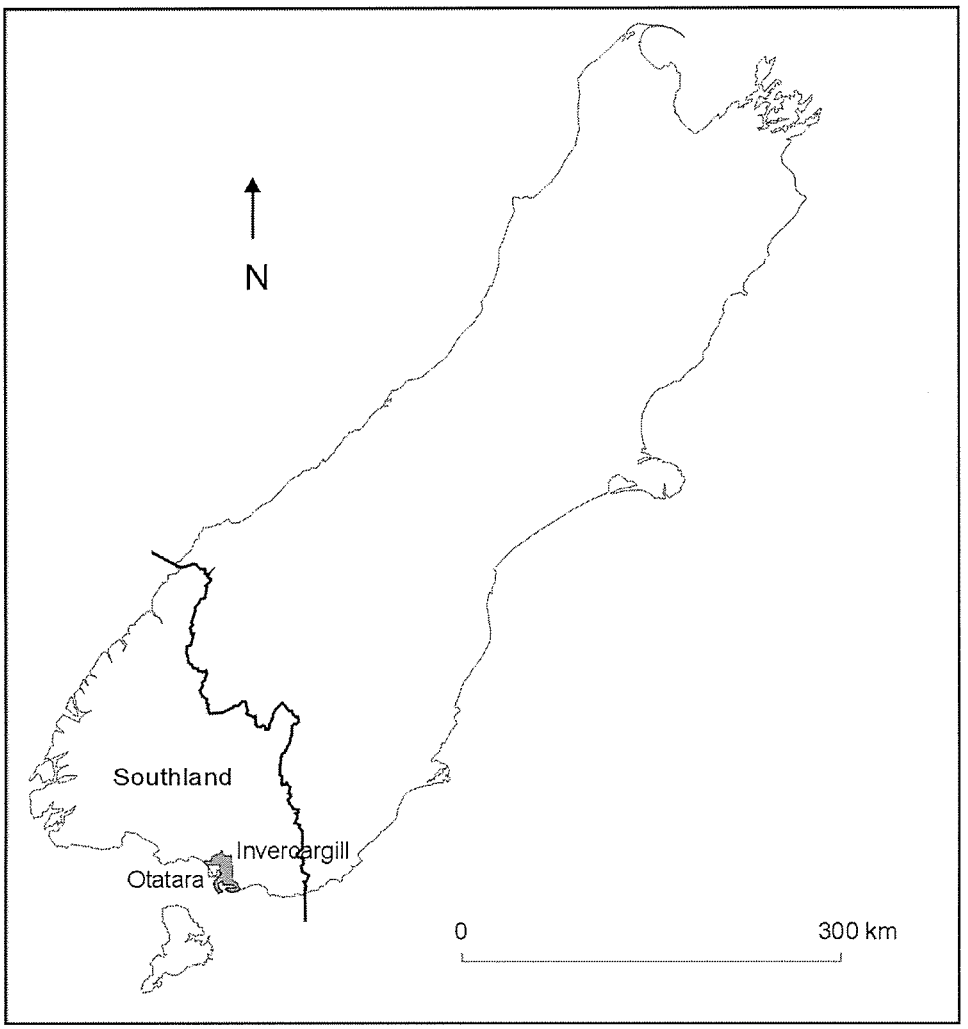


**Figure 3.1 Location map of Otatara, within Southland Region and Invercargill District**

## 3.2.2 Land use history

Norton (1996; in press) outlined the history of forest fragmentation and residential development at Otatara. The peninsula was entirely forested in 1865 (Norton, 1996) but has since experienced clearance and fragmentation. Norton identified two periods of forest modification, each associated with different phases of land use.

From 1865 until after World War II, possibly until the 1960s, forest removal was motivated by demand for farmland. Most clearance took place between 1865 and 1947, by which time the forest was 38% of its original extent (Norton, 1996). The outcome was a landscape of discrete forest patches in a matrix of exotic pasture (Norton, in press).

Most forest remnants at Otatara have been selectively logged at some time in the past (Norton, 1996). It is not known when the first sawmill at Otatara opened, but at least one, near the Oreti River bank, was operational in the early 1870s. By the late 1880s there were several mills in the area. The last was established in 1935, but it is not clear when commercial logging ceased (Matsui, 2000).

The second period of forest modification began in the late 1940s (Norton 1996; Norton, in press). Clearance was slower and apparently motivated by demand for land for housing, rather than for pasture (Norton, 1996). There was been less change to forest extent, but remnants were changed from relatively intact, compact patches to more convoluted shapes, perforated by small clearings associated with residential development (Norton, in press). This phase intensified in the late 1960s and is continuing.

### 3.2.3 The current landscape

Most of the original vegetation on the Southland Plains was cleared. Otatara is unusual in that some forest remains, although the area is close to an urban centre and development pressure is high (DoC, 1998; Matsui, 2000). The current landscape is a mosaic of three distinctive land covers: agricultural, residential, and indigenous vegetation. Sheep farming is the dominant form of agriculture in Southland, with some forestry, horticulture and dairy farming (SRC, 1997). Most agricultural land at Otatara is pasture, supporting sheep and some dairy cattle.

From entirely forested in 1865; forest patches now cover approximately 21% of the peninsula (Norton, 1996; Figure 3.2). There are over 100 patches ranging from 0.2ha to 55ha, with an average size of 2.6 ha. Despite fragmentation, the forest supports many birds, including kereru (*Hemiphaga novaeseelandiae*), bell-bird (*Anthornis melanura*), fernbird (*Bowdleria punctata*) and tui (*Prosthemadera novaeseelandiae novaeseelandiae*) (DoC, 1998).


**Figure 3.2 Map of Otatara showing the location of forest patches and study edges (Pasture - green; Recent residential - violet; Mid-aged residential - dark blue; Old residential - pale blue).**

The forest canopy is dominated by podocarp, particularly totara (*Podocarpus totara* and *P. halii*) and matai (*Prumnopitys taxifolia*), together with rimu (*Dacrydium cupressinum*) and kahikatea (*Dacrycarpus dacrydiodes*) and various angiosperm trees: pokaka (*Eleaocarpus hookerianus*), five finger (*Pseudopanax colensoi* var. *ternatus*), lemonwood (*Pittosporum eugenioides*), kohuhu (*Pittosporum collensoi*), tree fuchsia (*Fuchsia excorticata*) and matipo (*Myrsine australis*) (Norton, 1996). Manuka (*Leptospermum scoparium*) dominates disturbed areas. Common subcanopy and understorey species are kaikomako (*Pennantia corymbosa*), various *Coprosma* species, native jasmine (*Parsonsia* spp.) and many ferns (Bill, 1999).

Several environmental weeds are common. Sycamore (*Acer pseudoplatanus*), Darwin's barberry (*Berberris darwinii*), ivy (*Hedera helix*) and Chilean flame creeper (*Tropaeoleum speciosum*) have been noted as posing a particular threat to natural character as they can establish in intact forest (Norton, 1996; Bill, 1999).

There are several forest types, reflecting age and topography of the dunes (Norton, 1996). The youngest dunes support totara-dominated forest, with shrubs and wetland vegetation in the slacks. Matai - followed by rimu and kahikatea, then broadleaf canopy species - become progressively more common on older dunes. The oldest dunes, and the older slacks and sand plains, are covered with mixed podocarp-angiosperm forest, featuring rimu, kahikatea and pokaka. Anthropogenic disturbance - fire and logging - has modified this pattern so that totara, which is adapted to regeneration after disturbance, dominates the forest on some older dunes (Norton, 1996). Matsui (2000) created age-class distributions of *Podocarpus* spp. for some of the larger forest patches in the area, showing that most trees are less than 150 years old, while some are very much older. In summary, forest composition varies across Otatara (Matsui, 2000). The composition of each patch investigated in this research is noted in Chapter 5.

Residential dwellings at Otatara range from before World War II, when they were initially farm homesteads or holiday cottages, to more recent construction (table 5.1). There are several areas of recent subdivision and development - even though the population of Invercargill is currently declining (ICC, 1998) - and development may continue as people who work in urban centres move to rural areas at the urban periphery (Norton, in press). Otatara offers opportunities for residential or lifestyle properties in an atmosphere of peace and naturalness (ICC, 1998).

## 3.3 Conservation at Otatara

Several groups currently participate in conservation of indigenous vegetation at Otatara. Three of those are government bodies: the Department of Conservation, the Southland Regional Council and the Invercargill City Council. Local residents and conservation interest groups are also actively involved. Most forest at Otatara is privately owned and managed under the RMA. The forest at Otatara has been classed as of 'national significance' in two ecological assessments (Bill, 1999; Norton, 1996), and all groups involved in forest management at Otatara are subject to Section 6 of the RMA (Chapter 1).

### 3.3.1 The Southland Conservancy of DoC

As noted above, DoC has responsibility for the control of weeds on the conservation estate (DoC, 1998). It manages one forest patch at Otatara (the South Scenic Reserve) and may be involved in forest preservation and weed control through contributions to the Regional Pest Management Strategy or liaison with local councils and landholders (DoC, 1998).

The Conservation Management Strategy (CMS) for Southland sets out general information about forest conservation in the Southland Plains Ecological District, including Otatara (Norton, 1996) - but concentrates on large tracts of land administered by DoC and on highly threatened species (DoC, 1998). It identifies lowland forest as a habitat under-represented in the current set of protected areas. The Department seeks to remedy this by encouraging landholders to enter into conservation covenants or management agreements, and by administering funds to provide financial assistance for the protection of biodiversity on private land (DoC, 1998).

The CMS identifies elderberry as a particular threat to forest remnants on the plains. It also refers to scrub weeds, gorse and broom, but notes that these may form a seral stage in forest re-establishment (DoC, 1998). Some common weeds at Otatara (for example, Chilean flame creeper) are mentioned, but there are omissions, notably spindleberry and bittersweet. This may be because the CMS covers a very large area and those species are only pests in one area. The Department undertakes to monitor the spread of exotic species and conduct research to identify control priorities (DoC, 1998).

### 3.3.2 The Regional Council and Regional Pest Management Strategy

Under the RMA 1991, Regional Councils have responsibility for matters of regional significance, water, soil, and air quality and utilisation, natural hazards, and the coastal zone (s30). The Southland Regional Policy Statement (RPS) identifies biodiversity as a matter of regional significance (SRC, 1997) and notes that, inter alia, introduced plants and animals may threaten regional biodiversity.

The RPS contains several policies regarding the protection of significant vegetation and habitat, including:

> Policy 2.5
> Reduce the adverse effects of pest plants and pest animals on:
> a biodiversity;
> b areas of significant indigenous vegetation; and
> c significant habitats of indigenous fauna. (SRC, 1997 p73)

Methods proposed to achieve this, and other conservation goals, are largely non-regulatory, including education, consultation, financial incentives and support for voluntary initiatives. Monitoring and data collection are also mentioned. However, those methods are not described in detail and it seems the Proposed Regional Pest Management Strategy (PRPMS), which becomes operational in May 2002, more directly guides weed control.

The PRPMS focuses on public liaison, provision of information, surveillance and monitoring, rather than direct control. Responsibility for plant pest control is transferred to the occupier of the land on which the weed occurs, although Council is involved in ensuring that responsibilities are met (Environment Southland, 2000).

It has been suggested that the Biosecurity Act 1993 does not provide a clear mandate for Regional Councils to minimise the impact of pests on indigenous biodiversity (MfE, 2000b), but the Southland PRPMS does not seem to be hindered by this. Its stated purpose encompasses environmental, as well as cultural and economic, impacts of pests in Southland (Environment Southland, 2000) and proposes a control strategy similar to that advocated by DoC (Williams, 1997): one that focuses on key pests and areas of special value.

The PRPMS identifies three classes of weed. 'Total Control Plants' are limited in distribution or density, so eradication is a feasible goal and land occupiers are obliged to destroy them. 'Containment Plants' are abundant, so eradication is considered impractical. The goal is to limit their spread and land occupiers must destroy plants that are likely to spread to other properties. Land occupiers are not subject to rules regarding 'Surveillance Plants', except that it is illegal to distribute, sell or propagate them. These are generally plants of potential concern, but about which little is known (Environment Southland, 2000).

The PRPMS states that 'High Value Areas' will be identified, to focus control on places where pests will be particularly detrimental (Environment Southland, 2000). High value areas had not been defined in March 2002 (K. Carruthers, pers. comm. 20/3/02). However, the proposed classification system refers to the presence of rare, endemic species or communities, as well as to economic and cultural features. Forests at Otatara seem likely to qualify as high value.

Environment Southland and DoC both identify the need for information regarding the distribution and spread of invasive plants (DoC, 1998; SRC 1997), but published research findings are scant. A local polytechnic student recently investigated weed invasion with the assistance of Environment Southland and DoC (Thompson, 2000). She noted the composition of woody plants in quadrats near the edge and in the interior of four forest remnants on the floodplains of the Matuara River. Significant weeds were gorse (*Ulex europeaus*), blackberry (*Rubus fruiticosis*), holly (*Ilex aquifolium*) and elderberry (*Sambucus nigra*) (ibid). Although based on a simple survey, the study suggested that weed abundance is greater at edge sites, as noted in the literature (Chapter 2). Woody weed plants were older and more abundant in quadrats located within 10 m of a forest edge compared to quadrats more than 10 m in from the edge.

### 3.3.3 The District Council

The Invercargill City Council (ICC) manages most publicly owned forest in Otatara, but has not published management plans pertaining to it. The Council's environmental weed control has been limited to spraying known weeds at reserve boundaries, spraying along walking tracks and clearing areas to prepare them for new plantings. The only control within forest has been in the Otatara Scenic Reserve, being cutting (and stump poisoning) of sycamore (R. Pagan, pers. comm. 14/3/02).

District councils have control over landuse and subdivision under the RMA 1991, so primary responsibility for the protection of indigenous vegetation and habitat on private land is effectively devolved to district councils (Jones et al., 1995). There is considerable variation in the stringency of protection to indigenous vegetation and habitat applied by district councils around New Zealand, and in how well it is supported by data describing local biodiversity (Froude, 1997). The ICC commissioned a formal assessment of indigenous vegetation and habitat within its boundaries for its District Plan. Forest at Otatara was described as having national significance as the best remaining representative of totara and matai sand dune forest in New Zealand, even though it is fragmented and threatened by environmental weeds (Norton, 1996). Consequently, the Council's Proposed District Plan (ICC, 1998) included strict rules for the protection of forest at Otatara.

The Proposed District Plan cited specific threats to vegetation and habitat, including vegetation removal or habitat fragmentation, changes to the water table, alteration of soil character, changes to the degree of wind exposure, and the impact of exotic plants and animals, which covers most potential impacts of residential development on nearby natural vegetation (refer to Chapter 2). Protection was to be achieved through consideration of these threats when granting consents - any activity with 20m of significant vegetation was deemed discretionary - and through non-regulatory means, including consultation, education, and rate remission for formally protected land. The Council also undertook to monitor the status of significant vegetation and habitat every five years (ICC, 1998).

All of Otatara Peninsula was scheduled as significant in this document. Many submissions objected to the blanket restrictions, so a second survey was commissioned in 1998 to more precisely identify natural areas. A variation to the Proposed District Plan was released in March 2001 (P. Gear pers. comm. 2001).

The second report (Bill, 1999) examined scheduled areas in greater detail. Significance was assessed with regard to representativeness, rarity or distinctiveness of species or ecosystems, landscape context of the site (size, shape, diversity of habitat types, and connectivity), and natural character (the degree to which the site was threatened by invasive species or human impacts). Aerial photographs and ground-based surveys formed the basis of a GIS that accurately delineated natural areas and was used to create planning maps in the Variation to the Proposed District Plan (ICC, 2001).

The major change in the Variation is in the more precise identification of significant areas of vegetation or habitat. It also provides more information about how 'significance' was assessed. The Variation is more explicit with regard to weed management. It specifies that exotic tree species are not appropriate in areas of indigenous vegetation, and advocates their removal (ICC, 2001). The paragraph dealing with financial matters specifies that funding will be directed to pest control on Council and private land (ICC, 2001, p7).

The Variation stresses the need to enhance landholders' attitudes toward conservation. It discusses matters to be considered in granting resource consents in detail, mentioning the relative significance of the area and its proposed restoration. This seems to clarify matters for landholders and to provide more flexibility, allowing opportunities for the resource consent process to marry development and conservation initiatives. Tools to promote voluntary conservation are emphasised - like disseminating information to landholders, liasing with conservation groups, and provision of financial incentives - but regulation as a means of ensuring protection is not abandoned (ICC, 2001).

Again, Otatara is distinguished as having great natural values and special policies apply there (ICC, 2001). However, rules for the protection of forest in Otatara are less strict. For instance, the 20m buffer zone is omitted, instead clearing or reducing the integrity of indigenous vegetation is a discretionary activity. The potential threat of residential development is addressed explicitly: any construction or subdivision in an area mapped as significant is discretionary (ICC, 2001). The efficacy of those rules will depend consent-granting officers' understanding of conservation issues.

### 3.3.4 Local property owners

Landholders in Otatara are required to control plant pests listed in the PRPMS. In addition, the Proposed District Plan requires them to seek resource consent for activities likely to be detrimental to indigenous habitat or vegetation.

As the Variation to the Proposed District Plan acknowledges (ICC, 2001), landholders play an important role in weed control and other aspects of biodiversity conservation. Their willingness to participate is essential to the success of policies for biodiversity conservation (MfE, 2000b). Many Otatara landholders are enthusiastic conservationists, with 13 properties subject to covenants under the Queen Elisabeth II National Trust (G. Munro pers. comm.

8/8/01), is a quasi-non-governmental organisation established in 1977 to protect and enhancing open space by encouraging voluntary initiatives (Jones et al., 1995).

There is also an active Landcare group, established in March 1999 with the aim of bringing the natural history and ecology of Otatara to the attention of residents and the wider community and to promote and facilitate the protection, restoration and creation of such features(C.West pers. comm.13/3/02). It has approximately 150 member households, that is, about 1/3 of the Otatara population (ibid). The group is involved in various conservation activities, ranging from assisting the local primary school in collecting, cultivating, and planting out locally sourced indigenous seedlings (A. Mitchell, pers. comm. 8/8/01) to weeding bees in public reserves.

## 3.4. Target weed species

This study concentrates on 21 environmental weeds selected by reference to publications that identify weeds of conservation significance for forests in Southland or Otatara. The PRPMS identifies 49 plant pests, that is, species judged:

> capable of causing serious adverse and unintended effect in relation to the region on one or more of the following:
>
> - economic well-being; or
> - the viability of rare or endangered species of organisms, the survival and distribution of indigenous plants or animals. Or the sustainability of natural and developed ecosystems, ecological processes and biological diversity; or
> - soil resources or water quality; or
> - human health or enjoyment of the recreation value of natural and developed ecosystems, ecological processes, and biodiversity; or
> - the relationship of Maori with the land, water, sites, waahi tapu and taonga
>
> (Environment Southland, 2000 p117).

The interaction between exotic plant species and indigenous communities is a major consideration in this definition "plant pest" status (consistent with the definition of environmental weeds in Chapter 1). Of the 49 species listed in the PRPMS, 19 were likely to be present in forest at Otatara. Weeds of other habitats (waterways, pasture or open ground), known to be restricted to a small part of the region, or not yet present, were not targeted. A

Landcare Group newsletter identified 11 priority weeds in Otatara (West and Rance, 1999). One (aluminium plant) was not listed in the PRPMS and is considered here. Table 3.1 (overleaf) describes the 20 species and bittersweet (*Solanum dulcamara*), which was observed with relatively high percentage cover at many sites, suggesting it may have the potential to act as a weed, although it is not generally regarded as a threat to indigenous biodiversity (C.West, pers. comm. 2001).

### 3.4.1 Characteristics of environmental weeds

Chapter 2 discussed which characteristics of plant communities may make them vulnerable to invasive species. Another theme of weed research is the identification of characteristics of species that make them liable to become invasive (Goodwin et al., 1998; Kolar and Lodge, 2001; Rejmanek and Richardson, 1996). Several techniques for identifying potential weeds have been explored. These usually involve documenting situations in which plants act as weeds and extrapolating the findings to other situations, or considering the biological characteristics of species that become weeds (Rejmanek, 2000). Weeds are often invasive in more than one area, which suggests that characteristics intrinsic to the species determine invasiveness in concert with characteristics of the invaded habitat (Reichard and Hamilton, 1997).

Most studies that have attempted to identify critical attributes of weeds have found that weeds often tolerate a wide range of conditions and have a history of invasion in other areas. They also tend to be unlike plants already present in the natural community, that is, of exotic genera, or different growth form and have traits that allow rapid, prolific reproduction: short juvenile stages, short time between large seed crops, small seeds, seeds that do not require treatment prior to germination, and the capacity for vegetative reproduction (Kolar and Lodge, 2001; Reichard and Hamilton, 1997; Rejmanek 2000).

Rejmanek and Richardson (1996) classified 24 species *Pinus* species as invasive or non-invasive. Three life history characteristics - relating to mean seed size, length of the juvenile stage, and interval between large seed crops - were included in a function that discriminated clearly between the two groups. The discriminant function was applied to a further 34 pine species and several angiosperm trees and distinguished between species known to naturalise and those for which no records of naturalisation were found. Some species, often those dispersed by animals, were wrongly classified suggesting that dispersal mechanisms may also be important in determining whether species are invasive.

**Table 3.1 The target weed species**

| Name | Form | Growth | Reproduction | Dispersal | Threat | Date of naturalis-ation | Area of Origin | Other notes |
|---|---|---|---|---|---|---|---|---|
| **Aluminium plant** *Galeobdolon luteum* | Creeping herb | Vigorous rapid spread | Vegetative | Human | Inhibits regeneration and excludes ground cover species. | 1988 | Europe, west Asia | A 'National Surveillance Plant Pest'. Included in the Otatara Landcare Group noxious weeds report Known as a garden escape. |
| **Bittersweet** *Solanum dulcamara* | Vine | | Summer flowers followed by scarlet fruits | | Insignificant (Owen, 1997). | 1924 | Eurasia, north Africa | Not listed in the PRPMS, nor as a National Surveillance Pest Plant, although other *Solanum* spp are included. |
| **Blackberry** *Rubus fructicosus* agg. | Woody vine | Good establishment, rapid spread | Summer flowers followed by black fruits; vegetative | Birds | Inhibits regeneration; alters vegetation structure. | 1867 | Northern temperate regions | Listed as a 'surveillance plant' in the PRPMS & as a National Surveillance Plant Pest. |
| **Contorta pine** *Pinus contorta* | Tree | Rapid growth in young plants. | Many small seeds produced. | Wind. | Invades disturbed forest, shrubland. Changes habitat composition and structure. | 1957 | North America | Listed as a 'total control pest plant in some of Southland & a 'surveillance pest plant' elsewhere in the PRPMS. |
| **Cotoneaster** *Cotoneaster glaucophyllus* | Large shrub | Rapid growth in high light, can persist in low light | Spring-summer flowers followed by red fruits; vegetative | Birds | Replaces natural vegetation in regenerating forest | 1982 | China | A 'surveillance pest plant' in most of Southland & a 'total control pest plant' in some areas under the PRPMS, & as a 'National Surveillance Plant Pest'. A popular garden plant. |
| **Darwin's barberry** *Berberis darwinii* | Shrub/ small tree | Good establishment in low light, rapid growth | Spring flowers followed by purple fruits | Birds | Replaces natural vegetation in light gaps & at edges | 1946 | Chile, Argentina | A 'surveillance pest plant' in most of Southland & a 'total control pest plant' in some areas in the PRPMS Often used as a hedge plant. |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Elderberry** *Sambucus nigra* | Small tree | | Massed white flowers in spring, then black fruits. Prolific | Birds | Excludes other spp. in disturbed forest. Litter can inhibit seedlings | 1867 | Europe, west Asia, north Africa | Listed as a 'surveillance pest plant' in the PRPMS. |
| **Chilean flame creeper** *Tropaeolum speciosum* | Vine | Perennial but dies back in winter, rapid growth. | Scarlet flowers in summer, then dark blue fruits, vegetative. | Birds | Blocks light to understorey plants, increases load on canopy | 1958 | Chile | Listed as a 'surveillance pest plant' in the PRPMS.<br>A common garden escape. |
| **Green Daphne** *Daphne laureola* | Shrub | | Flowers in summer then black fruits | Birds. | Invades disturbed forest | 1959 | South west Europe, north Africa | Listed as a 'surveillance pest plant' in the PRPMS<br>Often associated with settlements or cultivated areas. |
| **Ground ivy** *Glechoma hederacea* | Herb | Mat-forming | Vegetative spread only. | Human | Outcompetes indigenous ground-cover & suppresses regeneration. | 1878 | Temperate Eurasia | Often cultivated, & a known garden escape. |
| **Hawthorn** *Crateagus monogyna* | Small tree | High rates of establishment & growth | Spring flowers then red berries; prolific. | Birds. | Invades shrubland & disturbed forest; suppresses regeneration. | 1899 | Europe | A 'surveillance pest plant' in the PRPMS.<br>Often associated with hedges, roadsides & old dwellings. |
| **Himalayan honeysuckle** *Leycestria formosa* | shrub | Rapid growth but shade intolerant. | Flowers in summer, then purple berries. | Birds. | Often invades disturbed forest & shrubland. | 1878 | Temperate Himalaya | A 'surveillance pest plant' in the PRPMS. |
| **Holly** *Ilex aquifolium* | Small tree. | | Flowers in late summer.<br>Red berries produced in winter. | Birds. | | 1901 | Europe, west Asia, North-west Africa | A 'surveillance pest plant' in the PRPMS. |
| **Ivy** *Hedera helix* | Vine. | May establish in light-moderate shade. | Flowers March-May then black fruits; prolific in high light; vegetative. | Birds. | May invade intact or disturbed forest; forms dense mats suppressing ground cover & competes for light in canopy. | 1873 | Temperate Europe & Asia | A 'surveillance pest plant' in the PRPMS<br>Often planted in private & civic gardens & becomes established around abandoned properties. |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Montbretia** *Crocosmia x crocosmiiflora* | Herb. | Forms large colonies in open sites | Vegetative. | Human | Invades disturbed forest. Supresses regeneration & outcompetes extant plants. | 1935 | South Africa, tropical South America | A 'surveillance pest plant' in the PRPMS. A common garden escape. |
| **Old man's beard** *Clematis vitalba* | Vine. | Individual plants may live more than 30 years. | Flowers in late summer, very prolific. | Wind. | Excludes light & may cause mechanical damage to canopy species. | 1940 | Europe, south west Asia. | A 'total control pest plant' in the PRPMS. A 'national surveillance pest plant'. Originally planted as an ornamental species. |
| **Periwinkle** *Vinca major* | Herb. | Mat-forming. | Mainly vegatative | Wind, water. | Invades intact or disturbed forest, may suppress regeneration & outcompete extant plants. | 1870 | Eastern & central Mediterranean | A 'surveillance pest plant' in the PRPMS. A common garden escape. |
| **Spindleberry** *Euonymous europaeus* | Small tree | Shade tolerant. | Flowers in late spring-summer followed by limited numbers of seed. | Birds. | Invades disturbed forest. May cause minor changes in vegetation structure or composition. | 1958 | Europe - Caucasia | A 'surveillance pest plant' in the PRPMS. Often grown as an ornamental plant. |
| **Sycamore** *Acer pseudoplatanus* | Tall tree. | High rate of establishment, rapid growth. Seedlings are shade tolerant. | Numerous flowers in late spring, followed by seeds. Prolific. | Wind. | Invades disturbed forest. Outcompetes other species for light & may replace all canopy species. | 1880 | Central & southern Europe | A 'surveillance pest plant' in the PRPMS. Often deliberately planted. |
| **Tutsan** *Hypericum androsaemum* | Shrub | Rapid growth. | Flowers in spring – early summer followed by black fruits. | Birds. | May invade disturbed forest, or forest edges. Can replace understorey species. | 1870 | Western & southern Europe, Asia minor & north Africa | A 'surveillance pest plant' in the PRPMS. A 'National Surveillance Pest Plant'. |
| **Wandering willie** *Tradescantia fluminensis* | Herb | High rates of establishment & growth. Mat-forming | Spreads freely by vegetative reproduction | Human | May invade intact forest. Suppresses ground cover & prevents seedling regeneration | 1916 | Brazil | A 'surveillance pest plant' in the PRPMS. |

Note: empty cells mean that the information is not known. Data sources are listed in Appendix A.

Weed screening models can aid decisions about proposed plant introductions if they draw on information about the global distribution and climatic tolerance of species, as well as information about growth habit and dispersal mechanism (Kolar and Lodge, 2001; Pheloung et al., 1999; Reichard and Hamilton, 1997) but their utility is limited by lack of critical information for many species (Goodwin et al., 1999).

In addition, many environmental weeds do not have typical 'weedy characteristics'. A third of the weeds in New Zealand's conservation estate have no history of weediness in other countries (Lee, 1999). Environmental weeds cover a wide range of forms, including trees, vines, grasses, geophytes, and aquatic plants, and occur in most plant families (Williams and West, 2000). Environmental factors also control weed status (Buist et al., 2000; Riechard and Hamilton, 1997). It is evidentially important to consider relationships between potential weeds and the characteristics of a particular environment.

### 3.4.2 Weeds at Otatara

Information about the ecology of a weed species can contribute to understanding how it enters an indigenous community, which communities are likely to be at risk, and its potential effects on the natural values of the community (Williams, 1997). The following examples suggest why the characteristics summarised in Table 3.1 may be important.

Plant form or structure has considerable influence over how it will interact with and influence indigenous vegetation. For instance, environmental weeds that are trees, such as sycamore (*Acer pseudoplatanus*), are likely to overtop indigenous plants and limit the light that reaches them (Reid, 1998), while perennial herbs prevent the growth of indigenous seedlings by densely covering the ground (Williams, 1997).

The growth rate of a weed, the age at which it produces viable seed, and its average life span influences its impact on indigenous vegetation and the rapidity with which infestation might spread. Successful weeds tend to grow rapidly, produce viable seed at an early age and produce large numbers of seeds at frequent intervals (Reichard and Hamilton, 1997; Rejmanek and Richardson, 1996). The life span of an individual plant also determines its weedy potential. Longer-lived plants have more significant effects on invaded communities; for example, annual herbs are not a conservation problem in New Zealand (Williams, 1997). Plants that are becoming naturalised now are more often longer-lived than were the species

that became naturalised some time ago, so the potential impact of weeds on New Zealand biodiversity may be increasing (Timmins and Williams, 1991).

Modes of reproduction and dispersal determine how rapidly and in what manner an environmental weed may be expected to enter and spread through indigenous habitat. For instance, clonal plants, such as wandering willie (*Tradescantia fluminensis*) rely primarily on humans for dispersal (Owen, 1997). Generally, these plants spread slowly but when humans intervene dispersal is erratic and may cover great distances (Williams, 1997). It seems probable that the distribution of species spread primarily by vegetative means would show the clearest relationship to sources of propagules, such as the developed land at the forest edge.

Species that are spread by birds are unlikely to be limited by dispersal, that is, they may well have distributions unrelated to the initial source of plant propagules. Plants with fruits spread by animals disperse seeds over an area that can extend for several kilometres and is not easy to predict the direction or distance of their spread (Williams, 1997). Pines (*Pinus* spp.) and other weeds that spread via wind-dispersed seeds may also rapidly travel many kilometers, depending on the intensity and direction of the prevailing wind (Williams, 1997).

Table 3.1 also includes some historical information about the origins of the weed species, and the date of their naturalisation in New Zealand. In the present context, information about origins is provided from general interest, and is not likely to contribute to an understanding of how the species acts as an environmental weed. The approximate date a species was naturalised in New Zealand may be relevant because it determines how much opportunity the species has had to spread and become established as a weed (Rejmanek, 2000). It should be noted that while several of these species are known garden escapes there is no certainty that plants within forest at Otatara arise only from gardens. Many, especially hedge plants such as Darwin's barberry, may originate from naturalised populations on farms or other land uses.

# Chapter 4

# Methodology

The effect of landscapes' spatial structure on ecological processes is an important facet of contemporary ecology (Collinge, 2001), yet studies of weed invasion often overlook spatial context, which limits their applicability for planning and management (Pickett and Cadenasso, 2001). This thesis considers the influence of spatial context on weediness within forest patches in a matrix of developed land.

This chapter describes methods of data collection, laboratory and statistical analysis used to evaluate this. It has three sections. The first outlines the overall research design. The second describes methods used to obtain data concerning eight factors involved in 16 hypothesised links that might create a relationship between weed abundance in forest and residential development nearby. That is, methods to quantify the boxed elements in Figure 2.1, viz

- Degree of residential development in the matrix adjoining forest
- Number of weed species in the matrix adjoining forest
- Structure of the forest edge
- Distance from the forest edge
- Anthropogenic disturbance
- Soil fertility
- Light availability
- Weed abundance within the forest

The final section outlines the statistical techniques used to test the 16 hypotheses.

Chapter 3 described the physical geography of Otatara, pre-European vegetation patterns, and history of land modification. Otatara is appropriate for this research, being a landscape of indigenous forest and rural land that has been exposed to ongoing suburban development. The topography and substrate are reasonably homogenous and the forest is nationally significant and at risk from weed invasion (Bill, 1999).

## 4.1 Research Design

Vulnerability of different types of habitat to weed invasion may be researched through experimental manipulation or observation of existing patterns. Both techniques have potential value: observational to identify possible causes of weed distribution, and experimental to investigate the mechanisms of those causes (Jesson et al., 2000). This research relies on observation of existing patterns. Research based on experimentation can prove causal relationships (Naeem et al., 2000), but the gulf between experiments and complex, real world situations that can only be bridged by research based on observation (Gilbertson et al., 1985; Naeem et al., 2000).

It would be informative to monitor weediness of forest patches over a period of increasing residential development, but such research has exacting requirements. It needs sites that have been subject to residential development in adjacent areas (treatment), some that have not experienced development (control), and baseline records for those sites before residential development. That information was not available for Otatara. Mack (2000) reviewed methods of reconstructing historic weed distributions, but most - such as reference to herbarium collections - are inappropriate to a local scale. McCay (2000) used aerial photographs to reconstruct past distributions of an invasive tree, however, most environmental weeds cannot be identified from the coverage for Otatara, a common limitation of remote sensing techniques (Mack, 2000). Reports of weed distribution at Otatara from before 1985 are scarce and of variable utility (search of the DoC Southland Conservancy Resource Inventory conducted 18/4/01; Peter Johnson pers. comm. 19/6/01).

Age class histograms can be used to reconstruct past patterns of invasion (McCay, 2000). The age distribution of a species at a site indicates when invasion first occurred, when it was most intense, and so on, but this is only applicable to species that can be reliably aged, such as woody plants with annual growth rings. Further, to determine the age of such plants is a time-consuming and error prone process. Rose (1997) used abundance of a weed species as a surrogate for time since infestation, and a similar approach was taken here.

Lack of adequate baseline and the limitations of methods that reconstruct past distributions meant that an alternative research design had to be employed. Rather than comparing sites pre- and post- development, I assessed the current state of forest edges exposed to residential development for different periods. Statistical analysis was used to search for correlations, testing the hypotheses derived from the literature (Chapter 2)

This research design assumes that environmental controls on weed invasion are the same at all times, so analysis of data representing a snapshot of sites at different stages of development is expected to reveal whether nearby development exerts any influence over weed abundance. In fact, weed distribution may be limited by one factor in the early stages of invasion and by others once populations are established (Wiser et al., 1998). Using sites at different stages of development as a surrogate for the same site at different temporal stages also risks that inter-site variation, unrelated to adjacent landuse, may distort results. However, this is a necessary compromise used, for example, by Rose (1997; Rose and Fairweather, 1997), Clements (1983) and Moran (1984).

## 4.2 Field methodology

There were two stages of field data collection: identification of suitable study sites and collection of information regarding weed abundance and environmental characteristics at those sites. The identification of appropriate sampling sites and the methods used to assess weed abundance and environmental characteristics at those sites are discussed below.

### 4.2.1 Identification of field sites

The search for suitable sites focused on edges between forest patches and cleared land. Murcia (1995) claimed that insufficient replication is a common failing of research into edge processes. She suggested that edge age, structure, and orientation, matrix type, and forest management history could create significant differences in edge related patterns. For this study, field sites needed to represent a range of ages of residential development, with other differences held constant, minimised or taken into account.

There are many possible methods to identify study sites. These include reference to published maps (such as the Land Information New Zealand 1:50 000 Topographic Map Series), to maps produced by the Invercargill City Council (ICC); ground based reconnaissance, and consultation with local residents or staff of the Department of Conservation (DoC) or ICC. For this research, a 50-year run of aerial photographs was used to identify sites suitable for detailed field investigation. Low-level coverage of the study area was obtained for the years 1946/7, 1967, 1974, 1982, and 1996.

Figure 3.2 shows current distribution of indigenous forest at Otatara and the location of the 13 study sites. Each site was identified as a distinct forest edge in photographs from 1946/7 (coverage was incomplete for 1946, so in two cases a photograph from 1947 was used) and was present in every image, with minimal change in shape or location, through to 1996. Site P1 was not visible in the coverage from 1982, but did not appear to change between 1974 and 1996.

The 13 edges were selected to represent four types of land use (Table 4.1 and Figure 3.2). More replicates would yield clearer results (Waite, 2000), but the advantages of replication had to be balanced against the time available for field research and the limited number of edges apparently unchanged since 1946/7. Some studies have used more replicates (Boutin and Jobin, 1998: 78 edges), but others are comparable to this study (Rose 1997: 15 edges).

**Table 4.1 Classes of land use represented by selected sites**

| Adjoining Landuse | Nature | Replicates |
|---|---|---|
| Pasture | No development, remains exotic pasture | 4 |
| Recent residential | First houses built between 1982 and 1996 | 3 |
| Mid-aged residential | First houses built between 1974 and 1982 | 3 |
| Old residential | First houses built between 1946 and 1967 | 3 |

It was not always possible to find edges where residential development took place over a short period. Therefore classes of land use are defined by the first appearance of a significant building along the edge (some residents commented that holiday cottages had been present for sometime, but they not visible on early aerial photographs). For example, at sites O1 and O3, some properties meet the criteria for 'Old residential' while others are younger. All transects are from properties of known and specified age.

Aerial photographs show the distribution of indigenous forest and residential properties more accurately than available topographic maps and allow more rapid site identification than ground surveys or interviews. They also gave information about edge age. Disparity in ages could confound the results because edges evolve through time (Chapter 2). Photographs show that every edge studied is at least 55 years old, and historic maps of the area indicate that none existed in 1865 (Bill, 1999).

Forest remnants that are currently grazed tend to have an open understorey (Burns et al., in press). Aerial photographs did not indicate whether edges were open to grazing (it eventuated

that every study edge adjacent to grazed land was fenced). It was not possible to determine whether the forest patches had been subject to other exploitation, such as logging. This is a limitation of the chosen field design, but could only have been overcome by intensive archival research of each remnant's history.

To return to Murcia's (1995) points, the method of site selection minimised differences in edge age. It captured variation in the nature of the adjoining matrix, and edge structure. It did not account for variation in the management history of forest because obtaining this information would have been excessively time consuming. Neither did it account for variation in edge aspect, because the set of possible - in terms of age and adjacent land use - edges was too small.

Aerial photograph analysis provided additional information. Figure 3.2 was created from the 1996 coverage, which was at a scale of 1: 10 000 (NZ Aerial Mapping Ltd SN 9492 Runs A/1-6, B/1-6 and C/1-6). The photographs were electronically scanned and joined to create a single image. This introduced error because some joins are imperfect. The image was registered and rectified against base-layer coverages (1:50,000) for NZMS 262/16, Invercargill, using *ArcInfo 8.1*. Borders of indigenous forest or tall scrub patches were digitised and information regarding the spatial arrangement of forest was derived using *ArcView 3.2* (Chapters 3 and 5).

### 4.2.2 Sampling routine

The purpose of sampling was to quantify variations in weed abundance and environmental factors between forest edge and interior, and between the study sites. Any recognised routine that characterises the vegetation of a small forest patch could have been used. For instance, a systematic distribution of sample points, based on a notional grid laid over an entire habitat patch (as in Magee et al., 1999) and a random distribution of sample points within each patch were considered, but rejected in favour of sample points located along a transect. Distance from the forest edge, an important aspect of spatial context (refer to Figure 2.1), could be readily quantified by this design.

Transects are commonly used to sample vegetation along an environmental gradient (Gilbertson et al., 1985) and are a common way to measuring change from forest edge to interior (Boutin and Jobin, 1998; Brothers and Spingarn 1992; Burke and Nol, 1998; Didham and Lawton, 1999; Goldblum and Beatty, 1999). Another, simpler, strategy is to sample one point adjacent to the edge and another in the patch center (Woolley and Kirkpatrick, 1999),

but this only indicates the direction and strength of differences between edge and interior. The transect-based approach captures possible ecological clines.

Transects have practical advantages over randomised or grid-based quadrat distributions. Quadrats were readily and reliably located in the field. Analysis of results was also straightforward: quadrats were assumed to be related to only one type of landuse: that at the transect origin. However, this proved a problem. The assumption that the matrix and edge at transect origin are the only external influences on all quadrats along a transect might not always be true. In fact, some quadrats lay close to another edge with a different land use from that at the transect origin. Transects were positioned using the GIS to minimise this problem (see also section 6.5.1).

Three transects were set out per study site, except for sites P1 and R2 which had four (41 transects in total). All transects at residential sites started from different properties (except at sites R3 and M1 where three and two transects, respectively, were from the same property; their origins were more than 25m apart). Transects ran 50m in from the forest edge. A hand-held compass was used to determine direction derived from the GIS (Figures 5.1 to 5.8). Ideally, measurements should be taken further into the forest than the recognised limit of edge effects (Brothers and Spingarn, 1992), but that distance is not known for Otatara (Norton, 1996). The maximum extent of edge effects in New Zealand forest has been reported as 50m (Young and Mitchell, 1994) and 40m (Davies-Colley et al., 2000). A 50m transect seemed likely to exceed the range of major edge effects, and is the distance used by Norton (1996) in his discussion of fragmentation at Otatara.

Quadrats were located at 10 metre intervals from 0 to 50m from the edge. Each was 2x2m, a compromise between the better representation of larger sizes and the limits imposed by time and resources (Gilbertson et al., 1985). It is comparable to sizes used in other studies of weed invasion (Boutin and Jobin, 1998: 1x1m; Brothers and Spingarn, 1992: 4x5m; Goldblum and Beatty, 1999: 1x1m; Jesson et al, 2000: 5x1m) and edge effects (Davies-Colley et al, 2000: 10x10m; Young and Mitchell, 1994: 10x10m and 3x3m) made in forest. Because this study involves an ecotonal margin, rather than homogenous forest, it was not possible to plot species numbers against increasing quadrat size to determine optimum quadrat size (Gilbertson et al., 1985).

### 4.2.3 Characterising adjacent land uses

Three aspects of spatial context -degree of residential development, number of weed species nearby, and edge structure (Figure 2.1) - were assessed with reference to the property at each transect origin.

Time since construction of the first residential building was used to represent degree of residential development, which is a surrogate for many potential effects (Chapter 2). The date of initial development was obtained from conversations with landholders. Pastoral sites were coded as zero years since residential development.

Most studies of the influence of the matrix on weed abundance in habitat have used simple, qualitative, descriptions of land-use (Gilfedder and Kirkpatrick, 1998; Magee et al., 1999; Timmins and Williams, 1991). Sullivan et al (in prep.) measured the number of all exotic species in a settlement to indicate overall weediness in the matrix near forest reserves. That list represented the range of species that could potentially escape into forest, but required extensive plant identification.

Aggregate measures do not show whether exotic plants enter the forest from populations close to the edge or from populations in the general neighbourhood. There are many routes that an exotic plant may take to spread into a forest patch. Figure 4.2 (overleaf) illustrates some possibilities: A: spread into the forest from a source population adjacent to the forest; B: spread from a population on a nearby property; C: slow spread from a distant population (for example along a pathway of disturbance) and D: direct dispersal from a distant source (for example by birds or wind).

This study examined the presumed effect of weeds spreading into forest from the nearest property (pathway A on Figure 4.1). Few researchers have quantified weed abundance in the directly adjacent matrix. Burke and Nol (1998) applied their data collection method to quadrats in the adjoining field, 5m from the edge as well as to quadrats in the forest interior. Brothers and Spingarn (1992) and Moran (1984) also used quadrats to quantify vegetation composition on adjoining properties as well as in forest. Those strategies were deemed too intrusive to be applied to private gardens at Otatara. Instead, weed abundance on adjacent properties was quantified by recording the presence or absence of the target species (Chapter 3). This strategy did not capture the density or age of the weeds present, both of which are likely to affect total propagule output, but was rapid.

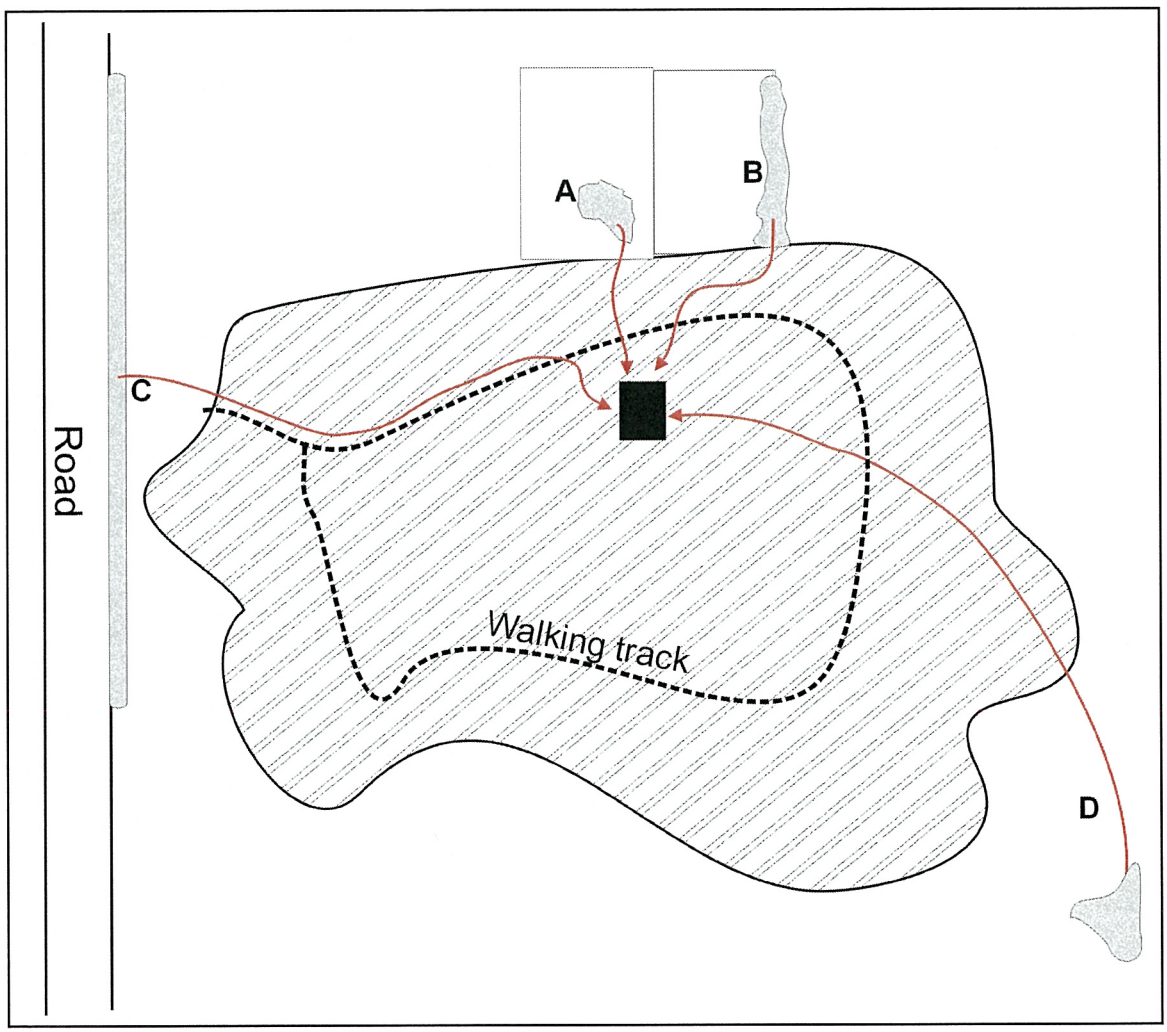


**Figure 4.1 Possible sources of an environmental weed present in a quadrat within a forest patch bordered by a range of landuses.**

The structure of the edge at each transect origin was also noted. Edges were classed as fenced or unfenced and open, partially closed, or closed (Figure 4.2).


**Figure 4.2 Edges classified as (A) open (B) partially closed and (C) closed**
A 2m scale rod marks the transect origin in each image.

### 4.2.4 Weed abundance

Weed abundance can be measured in many different ways, notably:

- density - number of individuals per species in a 1x1m quadrat (Goldblum and Beatty 1999)
- presence - which may be translated to a measure of species richness (Boutin and Jobin, 1998; Gilfedder and Kirkpatrick, 1998) or frequency by species (Brothers and Spingarn, 1992; Jesson et al., 2000; Larson et al., 2001)
- basal area (Rose, 1997)
- percentage cover (Boutin and Jobin, 1998; Burke and Nol, 1998; Gilfedder and Kirkpatrick, 1998; Jesson et al., 2000)

Density cannot be estimated unless discrete individuals of a species can be identified (Gilbertson et al., 1985) and was not used here because many of the target species are clonal. Rather, weed abundance was quantified by estimating the percentage cover of the 21 target species in each quadrat. Presence/absence and species richness could be derived from that data. Data was collected in October 2001, when most species were approaching full leaf so estimates of percentage cover are meaningful. Estimates of less than one percent were rounded up to one (as in Jesson et al., 2000). Larger estimates were rounded to the nearest percent to 10%, and to the nearest 10% after that. Visual estimates of cover are subjective and open to observer bias, but they are easily and rapidly obtained (Gilbertson et al., 1985) and indicate a weed's likely influence on the indigenous community (Burke and Nol 1998). Estimates may be simplified to accord with the Domin or Braun-Blanquet scales (Gilbertson et al., 1985) or specifically tailored to the study (Harper and MacDonald, 2001; Jesson et al., 2000) as in this case.

Total exotic species cover was also estimated. However, cover of individual exotic species, apart from the target species, was not noted, and some plants were not identified to the species level (notably exotic grasses). The decision to limit individual records to known environmental weeds reduced the time spent on identification of plants that are relatively uncommon and not currently recognised threats to indigenous biodiversity.

## 4.2.5 Evidence of anthropogenic disturbance

Data describing the intensity of disturbance was collected to test hypotheses 4, 14, 15 and 17.

Subjective measures are often used to describe disturbance (Hoehne, 1981). Matlack (1997) used a rating based on degree of soil and vegetation disruption: old, revegetated disturbances scored 1-3; intermediate levels 4-6; and recent disturbance 7-10. Rose (1997) also used a subjective ranking, where no disturbance scored 0; minor disturbance (a small number of rubbish items and damage to soil or vegetation covering <1% of the quadrat) 1; and major disturbance (a greater amount of rubbish, damage covering >1% of the quadrat) 2. A similar technique was applied here (Table 4.2).

**Table 4.2 Disturbance rankings.**

| Rank | Indication of the degree of disturbance |
|---|---|
| 0 | No evidence of disturbance. |
| 1 | < 3 items of rubbish; old or minor recent damage to vegetation; minor soil disruption. |
| 2 | >3 items of rubbish; substantial or recent damage to vegetation; soil disruption covering >25% of the quadrat. |
| 3 | > 5 items of rubbish; substantial and recent damage to vegetation; soil disruption covering >50% of the quadrat. |

Features such as streams, ditches and fences could constrain human movement and, hence, disturbance patterns within forest (Matlack, 1993). Edge structure might also influence where disturbance occurs: edges that are closed over by thick bushy vegetation normally deter human ingress. To minimise this complication, Matlack (1993) selected sites with similar edge structure. That was not appropriate here because edge structure can be a reflection of land use (Hypothesis 17).

## 4.2.5 Soil fertility

Soil was sampled at each study site for evaluation of Hypotheses 3, 6 8 and 13 (Chapter 2). Samples were taken from each quadrat on one transect per site (except site R2 where two transects were sampled): 84 in total. The top 10cm of soil was sampled. This layer usually contains the greatest nutrient concentrations and root mass (Wild, 1993), and was measured in other studies of weediness and soil fertility (Jesson et al., 2000; Wiser et al., 1998; Woolley

and Kirkpatrick, 1999). Samples were bagged and frozen before being transported in a chilly bin to the laboratory for analysis.

Concentrations of nitrogen, phosphorus and potassium are common indicators of soil fertility (Gilfedder and Kirkpatrick, 1998, Hester and Hobbs, 1992, Jesson et al., 2000, Woolley and Kirkpatrick, 1999). These are three of the essential macronutrient elements (Foth and Ellis, 1997; McLaren and Cameron, 1996) and tend to be enhanced by artificial fertilisation (Foth and Ellis, 1997). They were used to indicate soil fertility at Otatara.

Soil fertility indicators used in ecological studies vary. For instance, a recent study conducted in a New Zealand forest measured total phosphorus, total nitrogen and available potassium (Jesson et al., 2000). Woolley and Kirkpatrick (1999) assessed total nitrogen and available phosphorus and potassium, as well as pH and soil conductivity, while (Moran (1984) measured only pH and total soil phosphorus. The variation may be because tests of fertility are imprecise, particularly to determine plant-available nutrient levels (McLaren and Cameron, 1996) and researchers make different decisions about how to address this. The tests used here reflect the amount of nutrients available to plants. All are standard (Blakemore et al., 1987; Maynard and Kalra, 1993; Simard, 1993) and commonly used. The values found, however, may not be strongly related to plant performance (McLaren and Cameron, 1996).

In each analysis, a reagent blank and quality control (being a sample of known composition) were included with every 20 samples and measurements were repeated if quality control failed. Measurements derived from reagent blanks were subtracted from the values determined automatically to account for reagent contamination, but this was always very low.

Most nitrogen in the soil is unavailable to plants, being closely attached to organic compounds or fixed on clay minerals (Foth and Ellis, 1997). However, there is a constant flux between plant available and fixed nitrogen in the soil, making availability hard to quantify (McLaren and Cameron, 1996). Several measures, including total nitrogen (Jesson et al., 2000, Woolley and Kirkpatrick, 1999) and the C:N ratio (Wiser et al., 1998) have been used to quantify levels of nitrogen in the soil. In this research, concentrations of nitrate and ammonium ions were assessed; both are commonly used to indicate plant available nitrogen in a forest soil (Maynard and Kalra, 1993).

Forty ml of potassium chloride solution (2*M*) was added to 4g of field moist soil. After shaking for 30 minutes, the mixture was filtered. The filtrate was analysed automatically using a *Tecator Flow Injection Analyzer (FIAstar 5012 System)*. In this process, nitrate is

first reduced to nitrite with a copper cadmium column, then treated with two reagents that yield a purple azo dye. Colour intensity is proportional to nitrate concentration. Concentration was automatically calculated, using a calibration curve of concentration against light absorption at 540 nm (created with standards of known concentration). Ammonium ion concentration was determined simultaneously. The method was the same, with different reagents used to form a solution of colour intensity related to ammonium concentration. Again, concentration was calculated automatically, using a calibration curve of concentration against absorption at 590nm. Concentrations were corrected for dry soil using a moisture coefficient determined by weighing 5 g of moist soil and re-weighing after it had dried at 50 °C for 24 hours.

Soils were analysed for available phosphorus (phosphate ion) using Truog extracting solution (0.001*M* sulphuric acid buffered to pH 3 with ammonium sulphate). Fifty ml of solution was added to 0.25g of air-dry soil and shaken for 30 minutes before being filtered. The filtrate was analysed by a *Tecator FIAstar 5000 Analyzer*. Ammonium molybdate (0.5% solution in 1*M* sulphuric acid) and ascorbic acid solution were added, producing a blue compound, the colour intensity being proportional to phosphate concentration. Concentration was automatically determined by reference to a calibration curve of concentration against light absorption at 720 nm (Blakemore et al., 1987).

The concentration of water soluble and rapidly exchangeable (that is, plant available) potassium and other base cations were measured using ammonium acetate extraction (Simard, 1993). Air-dried soil (4g) was shaken for two minutes in 20ml of ammonium acetate (1*M*) solution and filtered. The filtrate was analysed using a *Varian SpectrAA 220 FS Atomic Absorption Spectrophotometer*. The *Sample Introduction Pump System* simultaneously added strontium chloride solution (20 000 ppm Sr), to suppress ionisation of the metal cations during flaming. Concentrations were automatically calculated by calibration against concentration standards.

Soil pH controls the availability of a wide range of nutrients and toxins, and thus regulates soil fertility (Foth and Ellis, 1997; McLaren and Cameron, 1996). It has been used as an indicator of soil fertility in other weed invasion research (Woolley and Kirkpatrick, 1999) and was assessed here. A slurry of 1g soil and 12.5ml 0.01*M* calcium chloride buffer solution was shaken for 5 minutes and left to settle for 10 minutes. The pH of the supernatant was measured with a *Radiometer PHM 201 Portable pH Meter* (Blakemore et al., 1987). For two samples the soil was so rich in organic matter that there was no supernatant and pH was not measured.

### 4.2.6 Light availability

Light availability within the forest was measured to investigate Hypotheses 2, 5, and 7 (Chapter 2).

*LI-190SA Quantum Sensors* (LI-COR, 1991) were used to measure photosynthetically active photon flux density (PPFD) in units of micromoles per square meter per second (LI-COR, 1991), the standard measure of incident light used in ecological research (Gendron et al., 1998). One sensor was positioned in the center of each quadrat, one meter above the ground. Average PPFD was recorded on a data logger for two 10 minute periods. The second sensor was positioned in an unshaded location outside the forest, and another data logger recorded 10-minute means of measurements made every five seconds. Two instruments were used so that a light measurement in the forest could be expressed as percentage of light in the open at that time: %PPFD (Davies-Colley et al., 2000; McDonald and Norton, 1992). In that manner, light availability can be compared among quadrats, although measurements were made in different external light conditions. Light availability was not recorded at 25 quadrats due to mechanical errors. Replicate transects were laid at sites R2 and P1 to compensate for this, so that a total of 221 measurements were used in analysis.

McDonald and Norton (1992) used a similar technique to assess light availability in podocarp forest on the West Coast, although they recorded PPFD over longer intervals. It is hard to characterise the total light environment of a forest because it varies in space and time (Gendron et al., 1998; Machado and Reich, 1999). Records of light availability over a long period best describe the light environment of a site, but more rapid measurement techniques have recently been developed (Gendron et al., 1998), such as measuring diffuse radiation only (using an instrument like the Li-Cor *LAI-2000 Plant Canopy Analyzer*, or selecting overcast weather conditions); hemispherical canopy photography (which determines the extent of the gaps through which light penetrates the forest canopy); and estimates of canopy density (Gendron et al., 1998; Machado and Reich, 1999).

Gendron et al. (1998) and Machado and Reich (1999) recently evaluated these techniques. Instantaneous %PPFD recorded in overcast conditions was found to explain approximately 88% of the variation in %PPFD recorded over an entire day (a more reliable indicator of overall light availability used) under a range of canopy types (Machado and Reich, 1999). The correlation becomes stronger when a longer 'instantaneous' measurement period is used (Comeau et al., 1998 cited in Machado and Reich, 1999). Gendron et al. (1998) found that 10-minute averages for overcast conditions satisfactorily explained 89% of variation in

%PPFD under different canopy environments over an entire growing season. In contrast, 10-minute averages for sunny conditions tended to under-estimate incident radiation at low values and over-estimate high values, but still explained 84% of variance (ibid). Short-term averages were only slightly less accurate than an instrument like the LAI-2000 (Gendron et al., 1998; Machado and Reich, 1999). Two ten-minute averages expressed as %PPFD were considered sufficient in this case.

### 4.2.8 Management history

Murcia (1995) suggested that forest management might confound research into edge effects, and management regimes have been shown to influence weed invasion in other areas (Gilfedder and Kirkpatrick, 1998). Since site selection did not ensure that all study sites had the same management history, it was important to account for the treatment of each patch. An attempt was made to do so, using information derived from many sources, including published histories, conversation with locals, and examination of records held by DoC and the Invercargill City Council (ICC).

## 4.3 Statistical analysis

This section describes statistical analysis of field data. The overarching aim of analysis was to assess the direction and significance of correlations between the eight factors (refer to Figure 2.1) involved in hypotheses derived in Chapter 2.

Statistics were used in three ways. Firstly, statistics that summarised the study environment were derived to describe environmental weed abundance; features of the surrounding matrix; and the forest interior environment. Secondly, non-parametric tests were used to examine correlations between two variables for hypothesis testing, and to clarify links between explanatory variables used in the final stage of analysis. Finally, multivariate analysis was used to identify which environmental factors contributed most to explanations of weed presence and abundance. All analyses were performed with *SPSS Version 10* (1999).

### 4.3.1 Descriptors of weediness

Exotic species richness is often used to indicate weed abundance or weediness (DeFerrari and Naiman, 1994; Gilfedder and Kirkpatrick, 1995). Both number of target species and the total number of exotic species present in each quadrat were used in this analysis, as well as total cover of target weed species and all exotic species, another indicator of overall weediness (DeFarrari and Naiman, 1994). Percentage covers of individual weed species were also used as response variables. Because the number of target species was limited, it was possible to specify their growth habits and dispersal mechanisms (Table 3.1) and consider individual species' responses to environmental factors.

The count of total exotic species is a conservative estimate because exotic grasses were not recorded as separate species. In addition, it may be a conservative indicator of weediness because several species such as lacebark (*Hoheria populnea*) and *Coprosma grandifolia* were not counted, although they were observed in several study sites and are not indigenous to Otatara (C. West, pers. comm. 7/10/01). *Muehlenbeckia australis*, which occurs naturally in the area and grows vigorously in many remnants, was excluded from these estimates, even though some conservationists regard it as a weed (Bill, 1999), and plants of similar status have been included in measurements of weed abundance used elsewhere (Batianoff and Franks, 1998).

### 4.3.2 Descriptive statistics

The first stage of analysis was to describe the field area with the data collected. Descriptive statistics were generated for the matrix (in terms of housing age and number of target weed species present for the properties at transect origins), the edge (in terms of structure and presence/absence of fencing), and the forest interior.

Brief descriptions of the indigenous vegetation and any known management information for each forest patch were compiled. The forest interior was also described by summarising disturbance, light availability and soil fertility data. Tables and graphs showing the most frequently observed and abundant (highest percentage cover) weed species for forest adjoining each landuse class were also created.

### 4.3.3 Non-parametric statistical tests

Non-parametric statistical tests are appropriate to the present study, where data sets for most variables contain many zeros and are not normally distributed (Gilbertson et al., 1985). Other weed invasion researchers have used these techniques for the same reason (for example, DeFerrari and Naiman, 1994). Another advantage of non-parametric analysis techniques is that they can be applied to ordinal data (Waite, 2000), such as degree of edge closure. Spearman's rho and Mann-Whitney *U* were used in this analysis.

Spearman's rho is a non-parametric test of the association between two quantitative or ordinal variables. The test compares the ranks of the two variables for every entity and generates a test statistic, rho, which indicates how much the value of one variable tends to increase as the other increases. A rho value of 1 indicates that the ranks of the two variables correspond perfectly, while -1 means that they are exactly opposite (Harraway, 1993). This test has been used in other studies relating weed cover to environmental variables, where the data were not normally distributed (Defarrari and Naiman, 1994).

The Mann Whitney *U* test assesses the null hypothesis that the two samples have the same distribution of a particular variable, and does so by comparing the sum of ranks for that variable for each sample (Harraway, 1993). It can be used to search for significant correlations between weed abundance and a binary environmental variable. DeFerrari and Naiman (1994) assessed the effect of landscape type by testing for differences between weediness of riparian and upland areas in this manner.

### 4.3.4 Search for correlation between two variables

The 16 hypotheses identified in Chapter 2 were assessed by testing for significant correlations between two variables. Spearman's rho test was used to search for correlations with continuous and ordinal environmental variables, while Mann-Whitney *U* was used to assess the effect of fencing, which was treated as a binary variable.

The status of the forest edge - originally recorded in words - was recoded to become an ordinal variable (open = 1; semi-closed= 2; closed = 3). Fence presence became a binary variable (present = 1; absent = 0).

Several hypotheses (5, 6, 9 and 15) involve distance from forest edge. Many techniques have been used to identify edge effects. For instance, the Helmert procedure - which compares

values at each sample point on a transect with every other point to find the point beyond which there are no significant difference - has been used by several authors to determine the maximum extent of edge effects (Burke and Nol, 1998; Fraver, 1994). It was not used here, where the aim was to determine if there is an edge-related pattern. Linear regression has been used to test for relationships involving distance from the edge (Harrison et al., 2001) but Spearman's rho was used here because data did not fit the assumptions of parametric analysis. Edge effects were also examined graphically. The mean and standard error of weed abundance and forest interior characteristics for each landuse class were graphed against distance from the edge (Chapter 5). This format is modelled on Rose (1997). Graphs were drawn in Microsoft Excel 2000.

As well as examining the 16 hypotheses, the Spearman rho and Mann-Whitney *U* were used to test for correlations between environmental variables. Such variables are often strongly interrelated which is important in the interpretation of results from multivariate regression (section 4.3.7). Explanatory variables will be excluded from the final model if they do not add to its explanatory power, even though they may be ecologically significant (Jesson et al., 2000).

The outcomes of correlation analysis are shown in a set of matrices, the typical format for presenting such results (Gilfedder and Kirkpatrick 1998; DeFerrari et al., 1994; Timmins and Williams, 1991; Woolley and Kirkpatrick, 1999). It should be noted, however, that the style of presentation used by Woolley and Kirkpatrick (1999) was not reproduced because it is misleading to represent only the significance of the interaction and not its strength.

Nine environmental weeds, including the five most common, were involved in more than one significant correlation with environmental variables (aspects of spatial context or forest interior). The third stage of data analysis, using many environmental variables to create general models of weed presence and abundance, was applied to the five most common species and to the aggregate measures of target and exotic species.

### 4.3.5 Multivariate statistical analysis

The third stage of statistical analysis was used to find which environmental factors are most important in determining weed abundance in forest at Otatara, and how much variation in weed abundance could explained by those factors. Multivariate statistics are used when sets of variables are involved either as predictors or as measures of response (McGarigal et al., 2000). Many statistical techniques, often variants of ordination or multiple regression, have

been used to search for relationships between weed abundance and environmental characteristics.

Ordination comprises techniques that organise sampling entities along gradients or axes derived from the sets of variables that describe each entity (McGarigal et al., 2000). Such techniques do not distinguish between response and explanatory variables (McGarigal et al., 2000). Boutin and Jobin (1998) use an ordination technique (Principle Coordinate Analysis) to identify differences in community composition for quadrats at various distances from the edge and adjacent to different landuses. The axes are created from data describing the abundance of dominant herbaceous species. Their work illustrates one limitation of ordination: it is not always clear what the axes - constructed simply to maximise the variation between the entities - represent (McGarigal et al., 2000). Boutin and Jobin (1998) were able to interpret one axis as representing a gradient from plants common in open, disturbed habitats, to those typical of more shaded, stable environments, but the second axis was less explicable.

Rose and Fairweather (1997) used two ordination techniques, Multidimensional Scaling (MDS) and Detrended Correspondence Analysis (DCA), where axes or dimensions were derived from species abundance data for a number of quadrats at several distances into bush reserves from residential developments of different ages. Both techniques showed that sites in forest adjoining suburbs of similar ages tended to have similar species composition, allowing the authors to draw conclusions about how residential development might lead to changes in vegetation over time. This example suggests that either technique could have been appropriate to this study. However, the authors' focus was on vegetation composition, and their data contained only two environmental variables (suburb age and distance to the edge). Application and interpretation of these techniques would be more complex with the large number of controlling environmental variables considered here.

It is possible to use ordination and other multivariate analyses on the one data set. Jesson et al. (2000), for instance, used DCA to describe variation in the weed flora of three different types of site (that is, only one environmental variable is considered) and then used Generalised Linear Modelling (GLM) - a form of multiple regression - to examine which of the several environmental variables best predicted the presence and abundance of exotic species.

Regression of a single response variable with many explanatory variables is a simple way of examining which environmental factor has most influence on weed abundance. It was used

here because it is particularly suitable for situations where many environmental variables may effect weediness. It produces results that are less ambiguous or difficult to interpret than ordination, and has been applied in research relating exotic species diversity to landscape or matrix characteristics (McKinney, 2001; Roy et al., 1999), relating the presence of individual plant species to landscape features (Bastin and Thomas, 1999; Roy et al., 1999); and relating weed abundance to forest environmental characteristics (Jesson et al., 2000).

### 4.3.6 Data transformation

Data describing weed percentage cover was positively skewed, and contained a large number of zero values, traits common to ecological data (Fletcher et al., in press). Multivariate regression analysis requires normally distributed data with few zeros (McPherson, 2001). Data sets can be transformed by simple functions to approximate a normal distribution (Waite, 2000), and that was attempted with the data from Otatara.

Mathematical transformations are often applied in studies of weed distribution and environmental factors. For instance, Deferrari and Naiman (1994) transformed their data for exotic species richness using a square-root function, which normalises positively skewed data sets (Wheater and Cook, 2000). Data may also be transformed using a logarithmic function, which normalises strongly positively skewed distributions (McKinney, 2001), or by taking the reciprocal of each value to normalise extremely positively skewed data (Wheater and Cook, 2000). Various transformations may be used to correct for other deviations (Wheater and Cook, 2000).

Fletcher et al. (in press) outlined a technique for analysing relationships between species abundance and environmental data. They advocate creating two sets of data: one describing presence or absence of the species or groups of interest, the other describing the abundance of a species when it is present. The first data set is analysed using logistic regression; the second is log-transformed and analysed using ordinary regression. Similarly, Jesson et al. (2000) created logistic, reverse, stepwise GLMs that relate weediness to environmental factors, using three response variables - presence/absence (a binary response function), frequency of occurrence in 100 subplots per quadrat, and percentage cover (excluding zeros) - for all exotic species and for four target species (15 models in total). This method is sensitive to the possibility that different factors control whether a species becomes established, and its dominance once established (Fletcher et al., in press).

That technique was applied here. Following Fletcher et al. (in press), I created new data sets, using (i) the presence/absence of the five most common environmental weeds, the presence/absence of any of the target species, and the presence/absence of any exotic species, and (ii) the percentage cover - where plants were present - of the five species, all target species and all exotic species. Data set (ii) was transformed using the function log[percentage cover+1]. A risk of this application is the assumption that data set describing species abundance has a lognormal distribution (Fletcher et al, in press). Visual inspection of normal Q-Q plots confirmed that transformed data had an approximately normal distribution.

In addition, model residuals were tested after regression analysis to confirm that the data met the requirements of regression analysis. Residuals were plotted against predicted values for each model and the normality of residuals was tested by inspection of normal probability plots (section 5.6.1).

### 4.3.7 Multivariate regression

Multivariate regression can be used to test for relationships between a response variable and various explanatory variables (an equation of the form y = c means that no relationship was found), and to see which of the many potential explanatory variables are most important in explaining the variation in the response (McPherson, 2001). Those applications are in keeping with the broad direction of an observational, rather than experimental, study such as this.

Following Fletcher et al. (in press), the data describing the presence of weeds was analysed using logistic reverse stepwise regression, and data describing the log (% cover when present) was analysed using linear reverse stepwise regression. In both cases characteristics of the matrix, edge, distance from the edge, disturbance ranking, and light availability were the explanatory variables.

Soil fertility data was not used in this stage of the analysis. Nonparametric correlation analysis showed that it was involved in only a few weak and barely significant correlations. Successful multivariate regression analysis requires a set of samples substantially larger than the number of explanatory variables employed in the analysis (McPherson, 2001). If regression analysis incorporated soil data the number of samples used would have been much smaller (soil was only sampled at a third of all quadrats). Omitting soil data also reduced the risk of collinearity, which may be caused by the inclusion of a very large number of

explanatory variables (McPherson, 2001) especially since bivariate analysis showed that most indicators of soil fertility were significantly correlated.

Reverse stepwise regression creates a model using all possible explanatory variables (step 1); the variable which contributes least to the explanatory power of the model is identified, and a new model is created using the remaining variables (step 2); the process continues until removing any further variables detracts from the model's effectiveness (SPSS, 1999). A variable is removed from the model if the significance of its F value is greater than a specified value. There is no theoretical basis for selecting an appropriate significance (McPherson, 2001), and in this case the default value of 0.1 was used (SPSS, 1999).

Multivariate regression can be used to create a predicative model (Wheater and Cook, 2000). Fletcher et al. (in press) described a method combining the regression equations for species presence/absence, and for abundance when present (created using the method described above) to derive a model that predicts species abundance from environmental conditions. This was not applied here, because the models will not be used as a tool to predict weed abundance for management, but to test whether a conceptual model relating weed abundance to a range of environmental characteristics is suitable for further consideration. Thus it was not necessary to verify models against independent field data.

# Chapter 5

# Results

This chapter has three purposes: to describe the Otatara landscape in terms of the data collected in the course of this research; to test hypothesised correlations between spatial context, forest interior conditions, and weed abundance; and to develop multivariate regression equations to indicate which environmental characteristics influence weed presence and abundance within forest patches in a matrix of rural and residential land uses.

## 5.1 Description of the study sites

The 13 study sites were located situated around eight patches of forest (Figure3.2). Aspects of the climate, geology, vegetation and history of land use of the study area were described in Chapter 3.

This chapter will begin by providing more detail about the individual forest patches. Images showing every forest patch and their immediate surroundings are included. Like Figure 3.2, these were generated from the GIS based on the 1996 aerial photographs. Study sites are shown in same colours as in Figure 3.2 (pale blue - old residential; dark blue - mid-age residential; purple - recent residential; green - pasture). Houses visited in the course of this research are marked with red squares, and the estimated age of housing is shown as a number of years. Transects are shown as yellow lines.


**Figure 5.1 Study sites O3, P2, P3 and surrounding land**

Otatara Scenic Reserve (Figure 5.1) is the largest forest patch in the area (approximately 55ha) and is regular in shape, although perforated by housing toward the northern edge (Figure 5.1). Three study sites - O3, P2 and P3 - are located around its borders. The O3 edge is partly on private land adjacent to the reserve, but property boundaries are not clearly marked. The edges at P2 and P3 directly border the reserve, P2 from the local school grounds, and P3 from a wide grass verge. Bill (1999) described this forest as a mixed podocarp forest containing kahikatea, pokaka, ribbonwood (*Plagianthus regius*), lemonwood and totara. Subcanopy species include wineberry (*Aristotelia serrata*), peppertree (*Pseudowintera colorata*), tree fuchsia, *Coprosma* spp., kohuhu and red mapou (*Myrsine australis*). The forest has been logged, and manuka shrubland (with a low canopy of manuka, and shrubby trees) dominates in several places (Bill, 1999). It is managed as a recreational reserve by the Invercargill City Council (ICC).

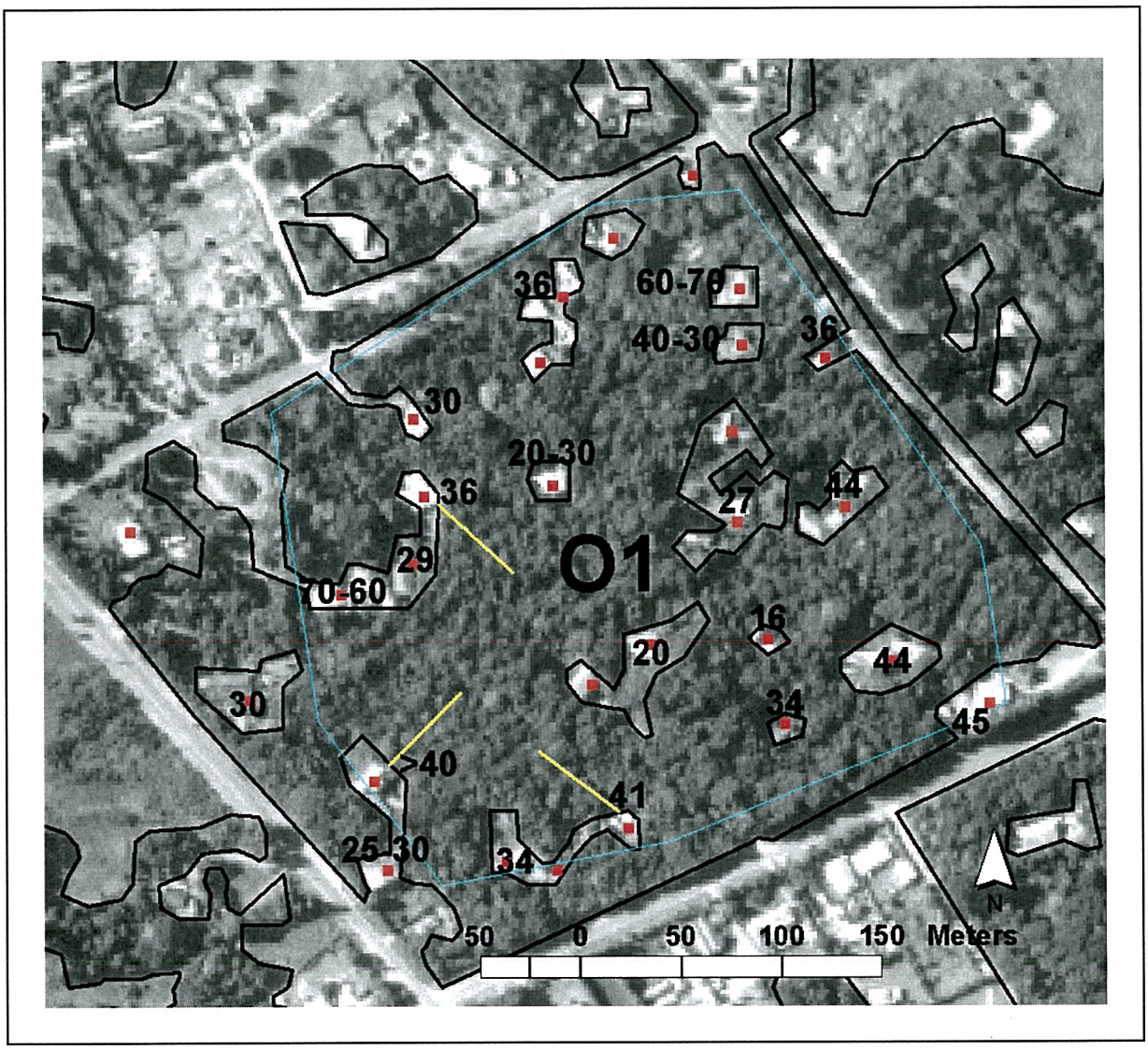


**Figure 5.2 Study site O1 and surrounding land**

Study site O1 is located in the forest between Taiepa Road, Marama Avenue South, Rata Road, and Grant Road (Figure 5.2). The patch is approximately 10ha in extent and highly perforated by residential development. Its canopy is dominated by totara, matai, kahikatea and broad-leaf species including lemonwood, putaputaweta (*Carpodetus serratus*) and pokaka. Common subcanopy species are tree fuchsia, *Coprosma* spp., red mapou, and seven finger (*Schefflera digitata*), while the ground layer is dominated by ferns (Bill, 1999). The entire patch is privately owned. Three Queen Elizabeth II trust covenants apply to parts of the patch, covering approximately 1.3ha in total.


**Figure 5.3 Study sites O1, R1, P4 and surrounding land**

Study sites O2, R1 and P4 are located on the edges of a long, narrow forest patch that is highly perforated on its eastern border (Figure 5.3). It covers approximately 22ha. Canopy species include kahikatea, totara, matai, rimu, miro (*Prumnopitys ferruginea*) and pokaka. The subcanopy is mostly peppertree, red mapou and *Coprosma aerolata*. Fern species and *Astelia nervosa* dominate the ground cover (Bill, 1999). It is believed that this patch has never been logged (Bill, 1999). It is mostly privately owned, the exception being Bowman's bush (1.5 ha) between Spence and Ruru Avenues, which is managed by the ICC.

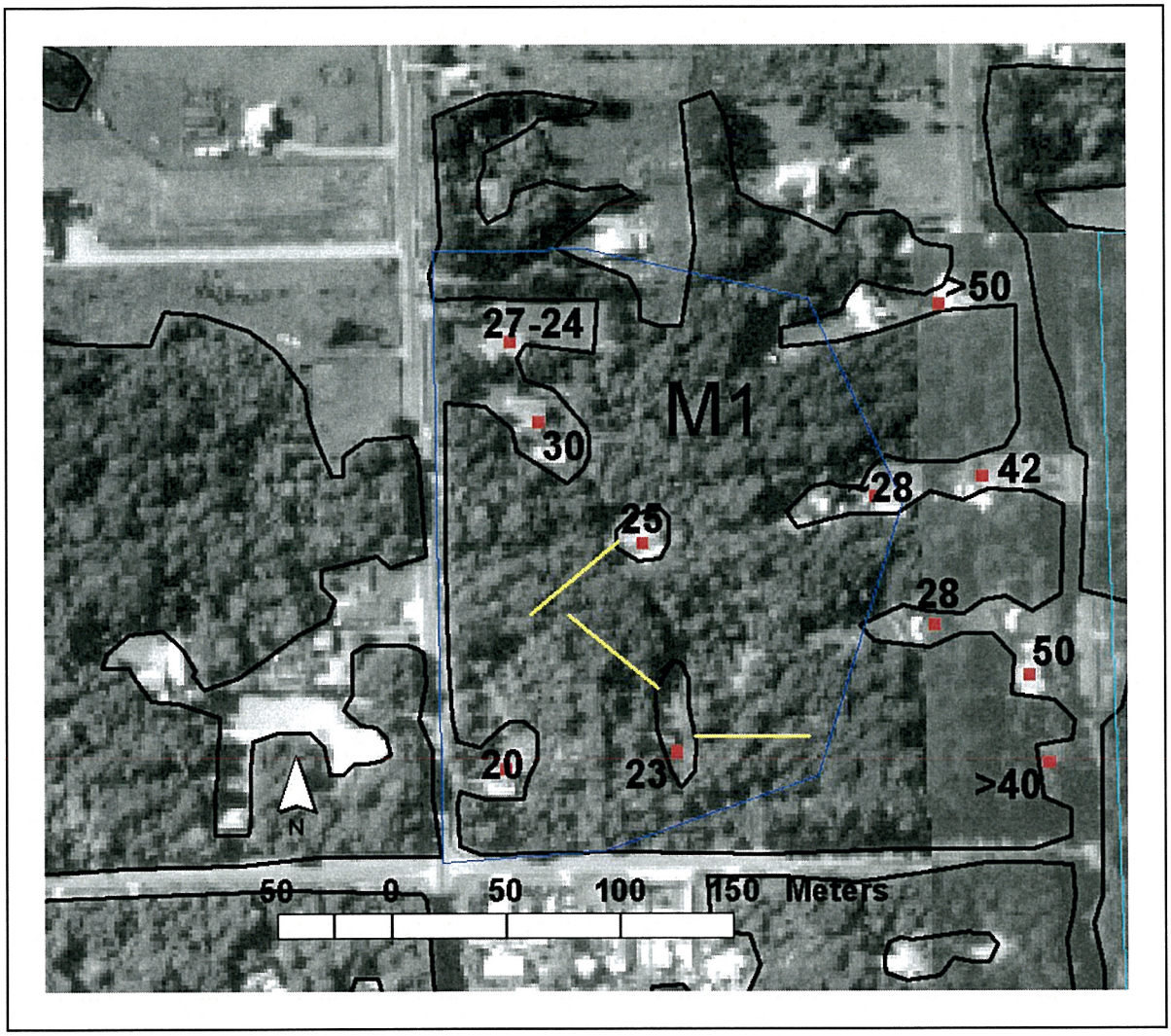


**Figure 5.4 Study site M1 and surrounding land**

One mid-aged residential development site, M1, is located in the forested area bordered by Ruru Avenue, Rakiura Parade and Ariki Avenue (Figure 5.4). This is a small patch (6ha) heavily perforated by clearings for houses and gardens. The forest canopy comprises totara, kahikatea, matai, and various broadleafed species, including wineberry, fuchsia, peppertree, putaputaweta, *Coprosma* spp., and wheki (*Dicksonia squarrosa*). Ferns dominate the ground cover (Bill, 1999). The forest is privately owned, with approximately 1.5ha protected by two Queen Elizabeth II Trust covenants. The extent of weed control is unknown, but a few landholders mentioned removal of some introduced plants from forest on their properties.

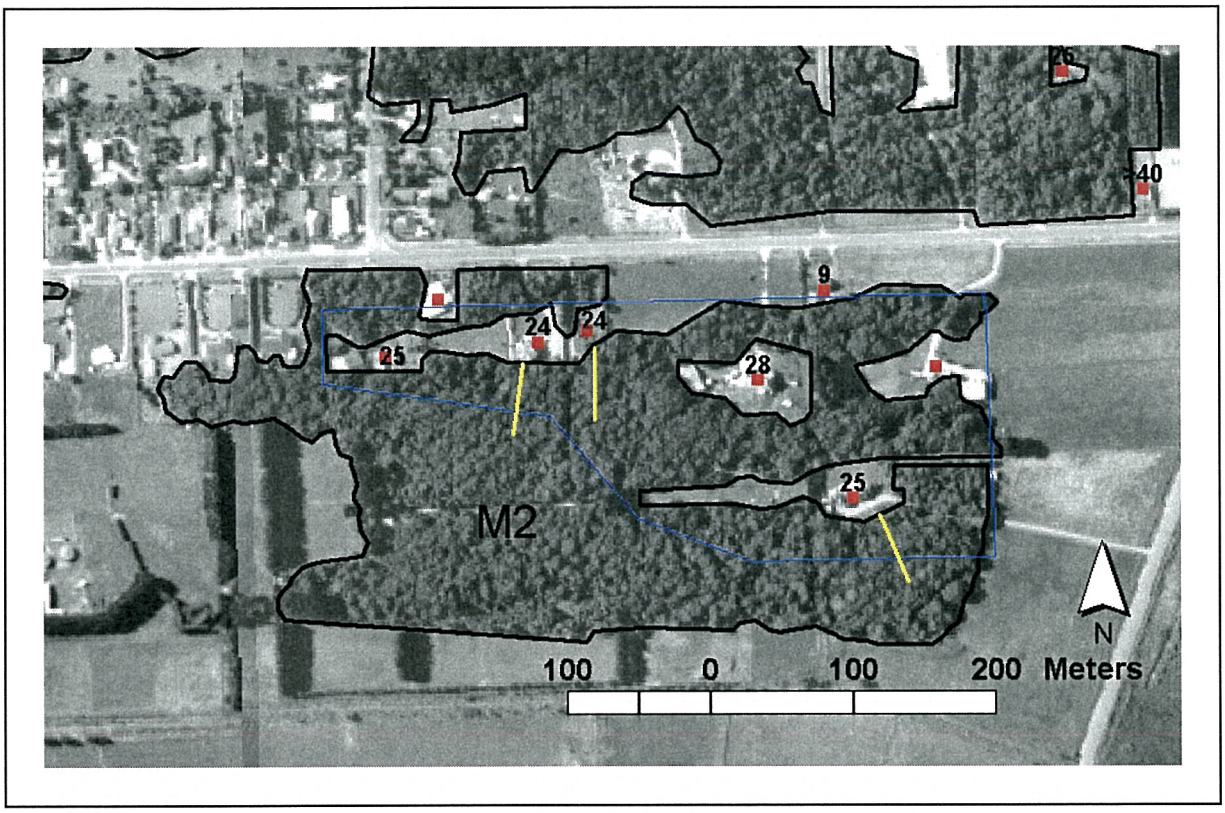


**Figure 5.5 Study site M2 and surrounding land**

The second mid-aged residential site, M2, is located in a 10ha forest patch south of Matua Road (Figure 5.5). Canopy species are totara with some kahikatea and matai. The understorey is relatively open and includes wineberry, *Coprosma* spp., tree fuchsia, lemonwood, kohuhu, koromiko (*Hebe salicifolia*) and others (Bill, 1999). The patch is privately owned and again, the extent of weed control within the forest is not known.

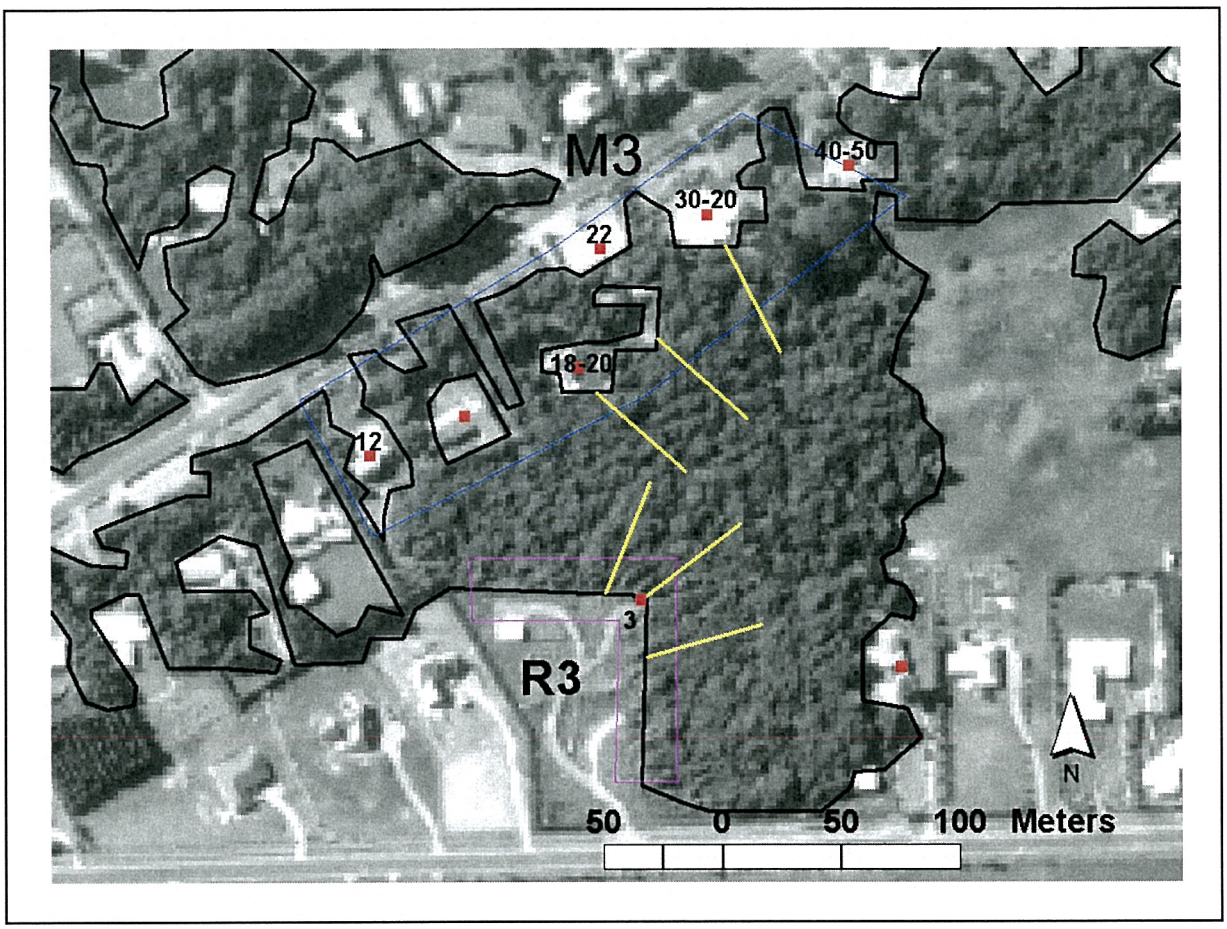


**Figure 5.6 Study sites M3, R3 and surrounding land**

Two study sites: M3 and R3, are located in a forest patch between Taiepa Road and Oreti Road (Figure5.6). This small stand covers approximately 6ha. It is not highly perforated, however; most development has occurred at the edges rather than within the forest. The forest is dominated by totara with kahikatea and matai. Various broadleaf species, including wineberry, tree fuchsia, peppertree and seven finger are present (Bill, 1999). The forest is privately owned.

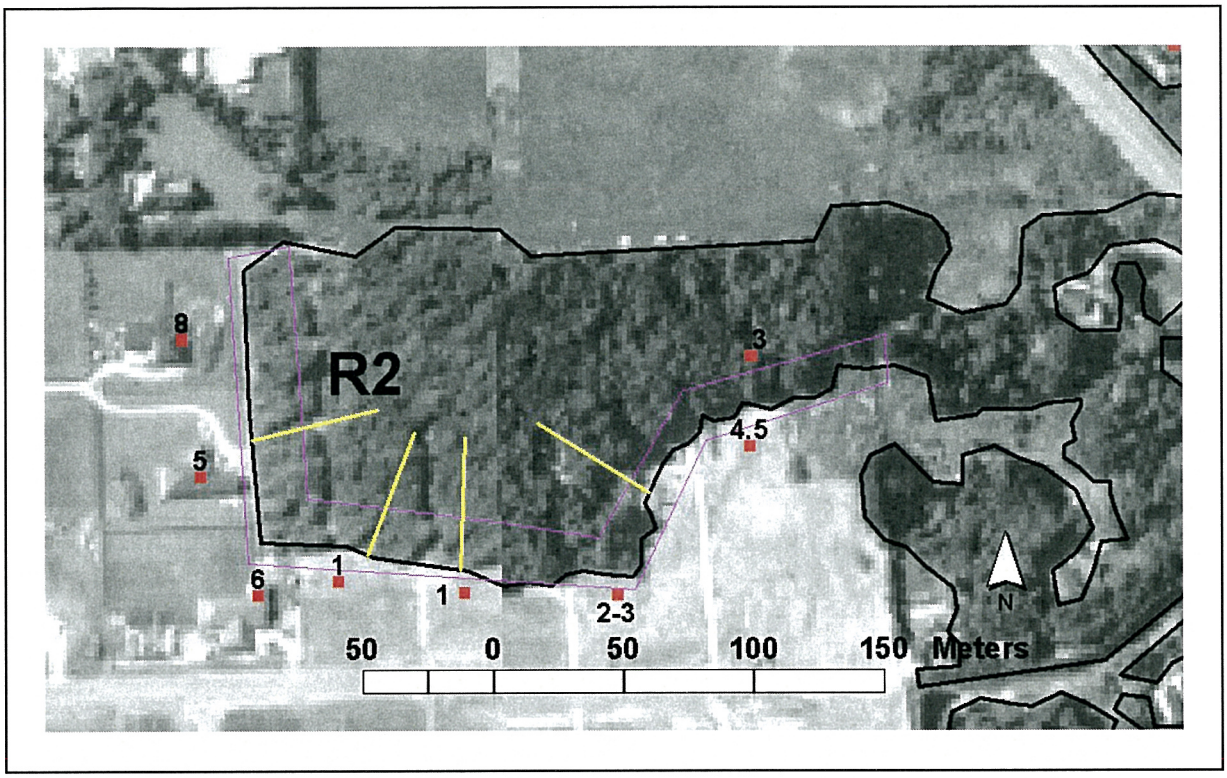


**Figure 5.7 Study site R2 and surrounding land**

The remaining recent residential development site, R2, is located at the end of Raeburn Avenue, in a small forest patch (4ha). It has a compact shape and is not yet highly perforated although it the area has been subdivided (Bill, 1999) and may soon be developed. Perforation has increased since 1996: several lanes have been cut in to the forest at right angles to the road, to permit provision of utilities to the new sections. This forest stand is of mixed composition, being dominated by totara, matai, kahikatea, manuka, peppertree and kamahi. Bracken (*Pteridium esculentum*) and other ferns are common in the ground layer, as are many exotic species (Bill, 1999).

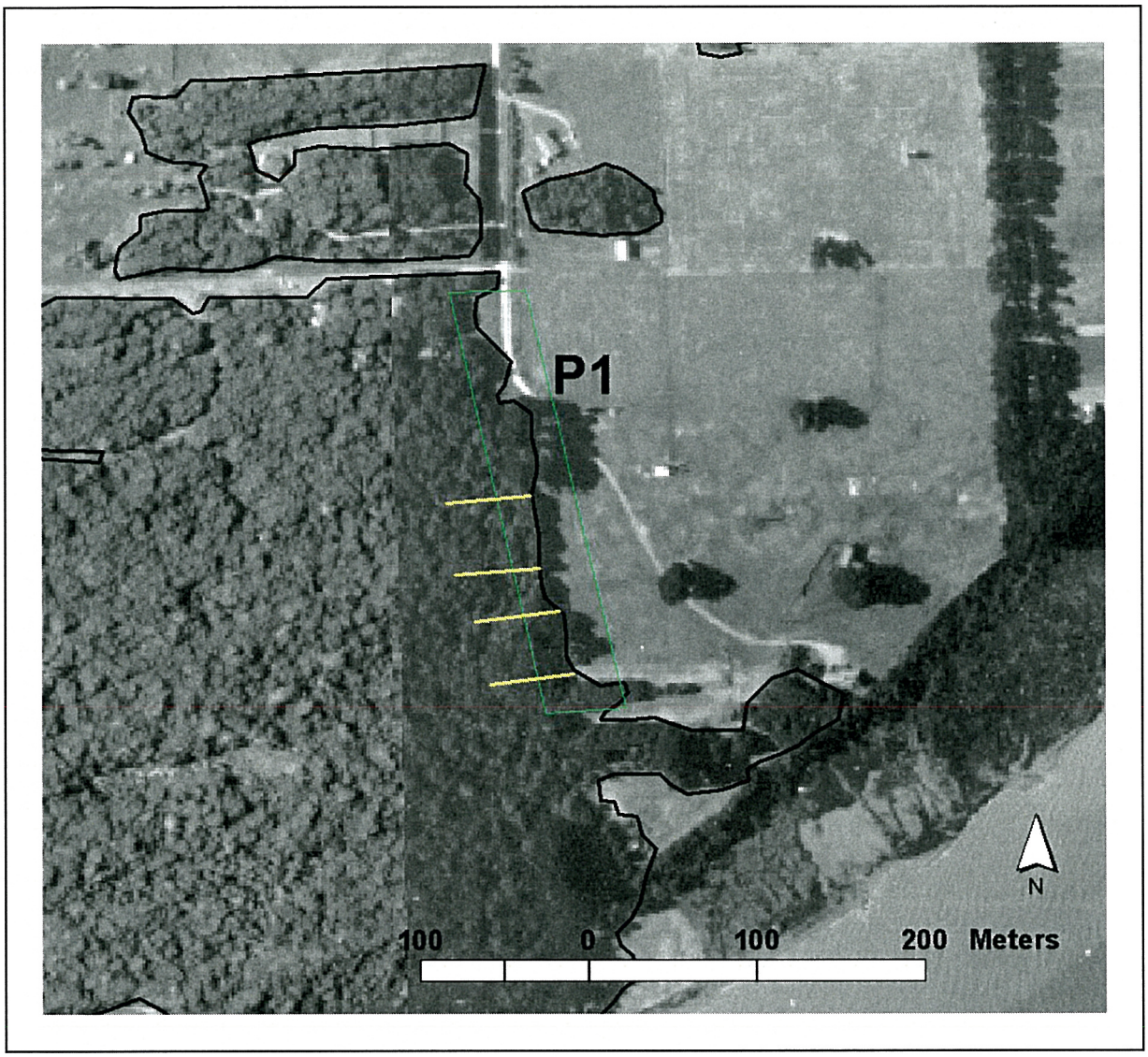


**Figure 5.8 Study site P1 and surrounding land**

Site P1 is in Otatara South Scenic Reserve, managed by the Department of Conservation (DoC). The forest covers approximately 24ha. The canopy is almost entirely dominated by totara, with some wineberry (Bill, 1999). The subcanopy is more diverse, although sparse, including *Coprosma* spp., tree fuchsia, peppertree and red mapou. Ground cover vegetation is also sparse. While the reserve is fenced, cattle may occasionally enter (ibid).

## 5.2 The Otatara landscape

This section draws on information collected in the field to describe the study sites. It first describes the spatial context of forest patches; chiefly environmental characteristics of properties from which transects originated and the structure of the forest edge. The two hypotheses relating residential development and other aspects of spatial context (Figure 2.1) are examined here. Secondly, the forest interior is described.

### 5.2.1 Characteristics of the matrix

Transects were laid out in 29 properties, and information from those represents the adjoining matrix. Residential development was of varying ages, even within land use class (Figures 5.1 to 5.8). The mean age of initial house construction on properties from which transects were taken is shown below.

**Table 5.1 Averages and ranges of house age by landuse class**

| **Landuse type:** | **Recent residential** | **Mid-aged residential** | **Old residential** |
|---|---|---|---|
| Mean house age | 3.1 yr | 23.7 yr | 49.2 yr |
| Minimum house age | <1 yr | 19 yr | 30 yr |
| Maximum house age | 6 yr | 28 yr | >75 yr |

Most properties at transect origins supported several target weeds in the area adjacent to forest. Two recent residential properties seemed to be completely free of known environmental weeds, as did one old residential property. The greatest number of target weed species observed at one property was 6 (Table 5.2).

**Table 5.2 Average and range for number of target weed species on properties by landuse class**

| Landuse Type: | Pasture | Recent residential | Mid-aged residential | Old residential |
|---|---|---|---|---|
| Mean number of target species | 3.4 | 2.3 | 3.2 | 5.6 |
| Minimum number of target species | 2 | 0 | 1 | 0 |
| Maximum number of target species | 5 | 6 | 5 | 6 |

In Chapter 2, it was hypothesised that:

*10. Number of environmental weed species in the matrix is correlated with residential development.*

This is supported by the field data from Otatara. House age and the number of target weeds growing on the property that adjoins the forest were positively correlated: older residential properties tending to harbour more weed species (Spearman's rho = 0.228 significant at 0.01 level, two tailed test).

The nature of the forest edge is another aspect of spatial context considered in this research. Two characteristics of the edge were recorded: presence of fencing and openness of vegetation structure. These varied within and among landuse classes (Tables 5.3 and 5.4).

**Table 5.3 Number and proportion of fenced and unfenced transect origins by landuse class**

| Number of origins | All sites | Pasture | Recent residential | Mid-aged residential | Old residential |
|---|---|---|---|---|---|
| Fenced | 15 | 10 | 1 | 1 | 3 |
| Proportion | 36.6% | 76.9% | 10% | 11.1% | 33.3% |
| Unfenced | 26 | 3 | 9 | 8 | 6 |
| Proportion | 63.4% | 23.1% | 90% | 88.9% | 66.7% |
| Total | 41 | 13 | 10 | 9 | 9 |
| | 100% | 100% | 100% | 100% | 100% |

In total, about two thirds of the edges were unfenced. Most edges bordering residential properties were unfenced and most bordering pasture were fenced. The only unfenced pasture edges were adjacent to a grass verge, where there was no chance of stock ingress.

**Table 5.4 Number and proportion of open, partially closed and closed transect origins by landuse class**

| Number of origins | All sites | Pasture | Recent residential | Mid-aged residential | Old residential |
|---|---|---|---|---|---|
| Open | 15 | 0 | 7 | 6 | 2 |
| Proportion | 36.6% | 0.0% | 70% | 66.7% | 22.2% |
| Partially closed | 10 | 2 | 2 | 1 | 5 |
| Proportion | 24.4% | 15.4% | 20% | 11.1% | 55.6% |
| Closed | 16 | 11 | 1 | 2 | 2 |
| Proportion | 39.0% | 84.6% | 10% | 22.2% | 22.2% |
| Total | 41 | 13 | 11 | 9 | 9 |
| | 100% | 100% | 100% | 100% | 100% |

Overall, there were comparable numbers of edges with open and closed structures. It was hypothesised (Chapter 2) that residential development would alter the structure of a forest edge:

15. *Increased closure of edge structure is negatively correlated with residential development.*

This is supported by data describing the structure of edge vegetation, even though edges close to recent residential developments are mostly open, while edges adjacent to older development tend to be wholly or partly closed. Most edges adjacent to pasture are closed and - overall - age of nearby housing is significantly negatively correlated with increasing edge closure (Spearman's rho -0.427; significant at 0.01, two tailed).

Fencing was also correlated with age of residential development: older residential properties are more often unfenced. Mann Whitney *U* test -the mean rank of development age for unfenced sites was 143.69 and the mean rank for fenced sites was 88.5 ($U$ = 3870; significant at 0.01, two tailed)

## 5.2.2 Characteristics of the forest interior

Great variation was noted in all recorded characteristics of the forest interior, the range of scores is typically large (Table 5.5). Disturbance was quite variable. A rank of 0 was assigned to 109 quadrats; 1 to 61, 2 to 35,and 3 to 41 quadrats (ranks are defined in Table 4.2). Light conditions ranged from almost the same as that measured in the open, to deep shade where only a small fraction of available light penetrated the canopy. The mean value indicates that light availability is generally very low and comparable to that recorded in other podocarp forests (McDonald and Norton, 1992).

**Table 5.5 Average and range for light availability and soil fertility measures from forest interior sites (to 2 decimal places).**

| Measurement | Mean | Maximum | Minimum | Standard deviation | Number of samples |
|---|---|---|---|---|---|
| Light availability (%PPFD) | 5.61 | 95.57 | 0.20 | 9.13 | 221 |
| Nitrate concentration (ppm dry soil) | 24.19 | 1339.32 | 0.00 | 146.12 | 84 |
| Ammonia concentration (ppm dry soil) | 26.48 | 176.23 | 1.11 | 28.97 | 84 |
| Phosphate concentration (ppm dry soil) | 38.12 | 501.50 | 3.80 | 90.09 | 84 |
| Potassium concentration (me/100g) | 0.43 | 2.69 | 0.06 | 0.40 | 84 |
| Calcium concentration (me/100g) | 10.84 | 46.48 | 1.64 | 8.67 | 84 |
| Magnesium concentration (me/100g) | 3.86 | 12.58 | 0.75 | 2.44 | 84 |
| Soil pH | 5.63 | 7.55 | 4.58 | 0.56 | 82 |

The concentration of major nutrients in soil samples taken from study sites at Otatara was varied, but average values are mostly moderate or high, indicating reasonably fertile soils. Concentrations of nitrates and ammonium ions were quite high, for instance greater than those recorded by Hester and Hobbs (1992) in Australian bushland, and than those recorded in

grassland soils (Whitehead, 1995 p 118). The concentration of Troug-soluble phosphate varied from very high to very low, but with a high average value (Blakemore et al., 1987). The average for potassium availability is low, but values range from very low to high. The average availability of Calcium and Magnesium was high and ranges from very high to very low, and very high to low, respectively. Average pH of the soil samples indicates moderately acidic conditions, with recorded values ranging from strongly acidic to slightly alkaline (Blakemore et al., 1987). Those values are comparable with standard values for Otatara yellow-brown sands (Chapter 6).

## 5.3 Correlations between forest interior characteristics and spatial context

On the basis of the theory of edge effects discussed in Chapter 2, disturbance, light availability and soil fertility may be expected to relate to conditions in the matrix and structure of the forest edge. The hypothesised linkages between aspects of spatial context and forest interior conditions are shown in sea-green on Figure 2.1and Table 5.6 is a matrix of correlations between the boxed factors.

Three hypotheses developed in Chapter 2 concern conditions within the forest in relation to distance in from the patch edge:

4. *Light availability is negatively correlated with distance from the forest edge.*

5. *Soil fertility is negatively correlated with distance from the forest edge.*

*14. Intensity of anthropogenic disturbance is negatively correlated with distance from the forest edge.*

Hypotheses 4 and 5 are not supported by field data from Otatara. Light availability does not show a significant correlation with distance. Most indicators of soil fertility also lack significant correlation with distance from the forest edge. Only phosphate concentration is positively correlated with distance from the edge, but the rho value is small and only just significant at the 5% level.

**Table 5.6 Correlations between the forest interior and distance to the forest edge, age of housing at the edge and edge structure**

| Forest environmental characteristics | Distance to the forest edge | Age of house construction | Edge structure |
|---|---|---|---|
| **Disturbance** | -0.428** | 0.244** | -0.395** |
| **Light availability** | -0.063 | 0.135* | -0.287** |
| **Nitrate ion concentration** | 0.112 | -0.002 | 0.236* |
| **Ammonium ion concentration** | 0.029 | 0.269* | -0.020 |
| **Phosphate ion concentration** | 0.218* | 0.151 | 0.094 |
| **Potassium ion concentration** | 0.044 | -0.071 | 0.213 |
| **Calcium ion concentration** | 0.118 | -0.059 | 0.225* |
| **Magnesium ion concentration** | -0.079 | -0.189 | 0.118 |
| **Soil pH** | 0.084 | -0.189 | 0.243* |

Notes: the entries give values of Spearman's rho correlation coefficient. ** significant at 0.01 (2-tailed); * significant at 0.05 (2-tailed).

In contrast, anthropogenic disturbance is negatively correlated with distance from the forest edge, indicating that disturbance is most intense close to the edge (refer to Figure 5.9). Thus, Hypothesis 14 appears to hold for Otatara, a finding which is supported by personal observation. Much of the soil trampling noted - by far the most common form of disturbance - seemed related to little used paths or tracks that start at the edge and peter out a short way into the forest.

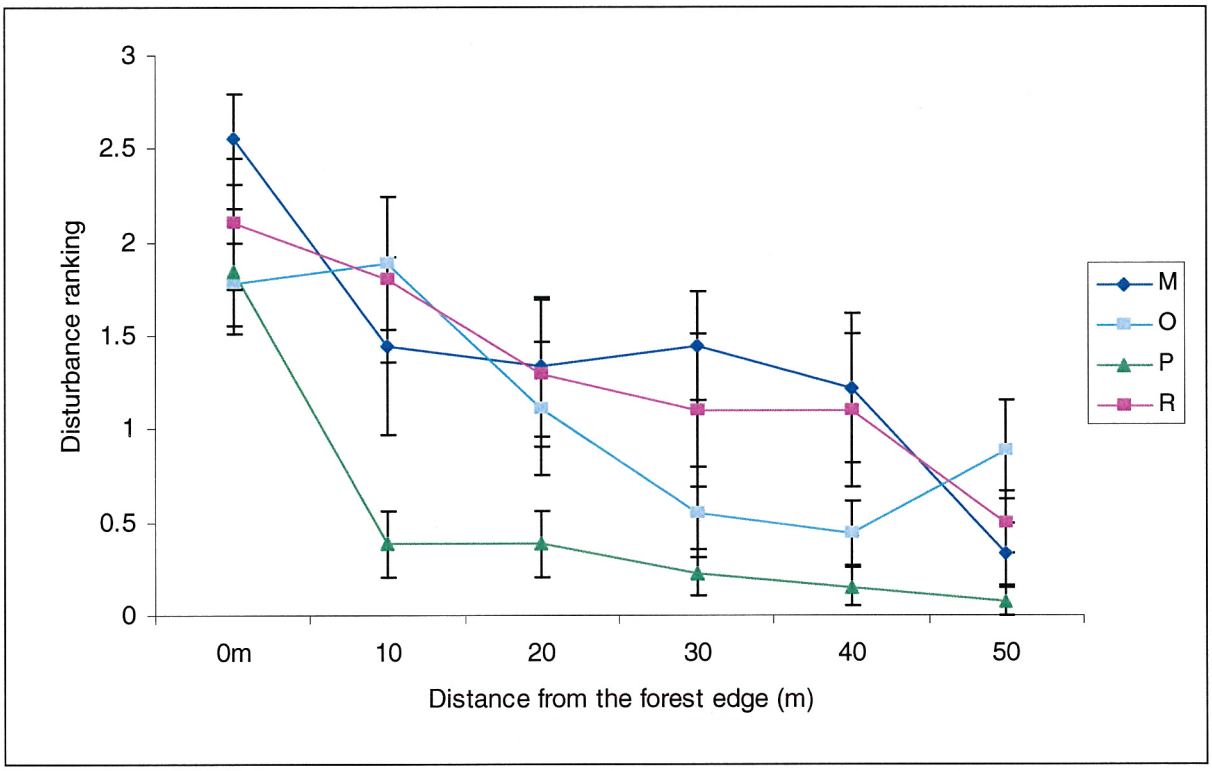


**Figure 5.9 Mean disturbance ranking against distance from the forest edge by landuse class**

Note: O = old residential development, M = mid-aged residential development, R = recent residential development, P = pasture. Bars show the standard error associated with each mean.

The literature reviewed earlier suggested that forest interior conditions could be influenced by landuse in the matrix adjacent to the forest. Two hypotheses concern this:

12. *Soil fertility is correlated with residential development.*

13. *Intensity of anthropogenic disturbance is positively correlated with residential development.*

Only one indicator of soil fertility was significantly positively correlated with the age of adjacent residential development: ammonium ion concentration. The correlation was not very strong or very significant so it seems best to reserve judgement on hypothesis 12.

In contrast, disturbance was much more intense in forest near older residential properties (Figure 5.9) so Hypothesis 13 is supported. Much of the observed disturbance seemed to result from activities of local residents, notably dumping of garden rubbish, construction of children's huts, creation of walking paths and removal of ferns for cultivation within the

garden 'proper'. The difference is strongest between forest adjoining pasture and forest adjoining residential areas, and less clear-cut between different age classes of residential properties. The hypothesis is also supported by a highly significant, although not very strong, correlation (Table 5.6).

Light availability is significantly correlated to the age of the adjacent property: the floor of forest near to older residential properties tends to be better illuminated. This may be because forest adjoining older properties tends to have more open edges and be more disturbed, both factors that are correlated with higher light levels.

Several researchers have proposed relationships between characteristics of the forest interior and the structure of the vegetation at the forest edge (section 2.3.2). It seemed likely that abiotic edge effects in forest at Otatara would be more pronounced where edges have more open structure. Further, the condition of an edge is expected to indicate the frequency of traffic into the forested area. Edges that are fenced or sealed are likely to be less often penetrated by humans or other domestic animals. Those proposals underly the following hypotheses:

6. *Light availability is negatively correlated with increased closure of edge structure.*

7. *Soil fertility is negatively correlated with increased closure of edge structure.*

16. *Anthropogenic disturbance within forest is correlated with edge structure.*

Hypothesis 6 is supported by the field data: light availability is negatively correlated with edge closure, indicating that where edges are less open, less light filters into the forest interior.

Hypothesis 7 was not supported. In fact, three indicators of soil fertility had positive correlations with edge closure, indicating that more fertile soils were associated with more closed edges.

Disturbance ranking was significantly negatively correlated to edge structure, indicating that forest close to open edges is subject to a greater intensity of anthropogenic disturbance. Hypothesis 16 can be accepted for Otatara. This could be a reciprocal correlation because more open edges should allow a higher influx of people and, therefore, disturbance into the forest while increased traffic, as indicated by high levels of disturbance, might be expected to maintain an open edge structure.

Whether or not a forest edge is fenced could also affect how far edge effects, particularly those associated with human activity, reach into interior forest. Table 5.7 presents the results of analysis using the Mann-Whitney test: a significant difference between mean rank of fenced versus unfenced transects for any particular variable shows that the presence of fencing is correlated to that variable.

**Table 5.7 Correlations between forest interior characteristics and presence of fencing at the edge**

| Forest interior characteristic | Mean rank fenced | Mean rank unfenced | *U* value |
|---|---|---|---|
| **Disturbance ranking** | 105.22 | 134.04 | 5375.0** |
| **Light availability** | 105.38 | 114.51 | 5302.0 |
| **Nitrate ion concentration** | 48.90 | 40.50 | 512.0 |
| **Ammonium ion concentration** | 34.10 | 45.13 | 472.0 |
| **Phosphate ion concentration** | 49.25 | 40.39 | 505.0 |
| **Potassium ion concentration** | 45.55 | 41.55 | 579.0 |
| **Calcium ion concentration** | 49.50 | 40.31 | 500.0 |
| **Magnesium ion concentration** | 48.33 | 40.68 | 523.0 |
| **Soil pH** | 51.25 | 38.35 | 425.0* |

Note: entries in the right-hand column give values of Mann-Whitney *U*. ** significant at 0.01; * significant at 0.05 (2-tailed).

The correlations are similar to those found between forest interior conditions and vegetation structure of the edge. There is no significant correlation between the presence of fencing and light availability, or many significant correlations involving indicators of soil fertility, the most notable exception being that soil was slightly more alkaline where edges fenced. Fenced edges, however, have generally lower disturbance rankings than unfenced edges, which also supports Hypothesis 16, and indicates that fences are an effective deterrent to people entering the forest.

### 5.3.1 Cross correlation of forest interior characteristics

There are several significant correlations between factors that represent environmental conditions within the forest at Otatara, particularly involving disturbance (Table 5.8). None of the hypotheses developed in Chapter 2 proposed such correlations, but they are discussed here because (i) they could clarify patterns of environmental weed distribution, and (ii) potential co linearity of explanatory factors should be considered in the application of multivariate regression analysis (section 5.6).

**Table 5.8 Correlation of forest interior characteristics with disturbance ranking**

| Forest interior characteristic | Correlation with disturbance |
|---|---|
| Light availability | 0.212** |
| Nitrate concentration in soil (NO3) | -0.268* |
| Ammonia concentration in soil (NH3) | 0.000 |
| Phosphate concentration in soil (PO3) | -0.299** |
| Potassium concentration in soil (K) | -0.200 |
| Calcium concentration in soil (Ca) | -0.333** |
| Magnesium concentration in soil (Mg) | -0.202 |
| Soil pH (pH) | -0.234* |

Note: entries in the right-hand column give spearman's rho correlation coefficient.
** significant at the 0.01 level (2-tailed); * significant at the 0.05 level (2-tailed)

The significant, positive correlation between light and disturbance ranking is to be expected as disturbed sites commonly have a more open canopy structure and/or less dense sub-canopy vegetation. Disturbance rank is significantly negatively correlated with concentration of nitrate ions, plant available phosphate and calcium in the soil. Increased disturbance is also correlated with greater soil acidity. This suggests that disturbance leads to decreased soil fertility, this may be because the organic litter layer is often thinner and patchier, and the soil structure is disrupted at disturbed sites, increasing the loss of nutrients through run off and leaching.

Concentrations of soil nutrients are almost all significantly positively correlated: soils rich in one nutrient tend to be rich in others, that is, generally more fertile. Positive correlations between soil pH and the availability of calcium, magnesium, nitrogen and phosphorus (below pH 6.5) are well known (McLaren and Cameron, 1996).

**Table 5.9 Cross-correlation of soil fertility indicators**

| | Ammonium | Phosphate | Potassium | Calcium | Magnesium | pH |
|---|---|---|---|---|---|---|
| **Nitrate** | 0.487** | 0.569** | 0.458** | 0.626** | 0.257* | 0.325** |
| **Ammonium** | - | 0.395** | 0.317** | 0.375** | 0.132 | 0.276* |
| **Phosphate** | | - | 0.547** | 0.655** | 0.469** | 0.273* |
| **Potassium** | | | - | 0.656** | 0.497** | 0.315** |
| **Calcium** | | | | - | 0.625** | 0.601** |
| **Magnesium** | | | | | - | 0.495* |

Note: entries give Spearman's rho correlation coefficient. ** significant at the 0.01 level (2-tailed); * significant at 0.05 level (2-tailed)

# 5.4 Spatial context and weed abundance

This section will begin with a general account of the weed flora of the forest interior at Otatara, then present statistical analysis of weed abundance and the spatial context of quadrats.

## 5.4.1 Description of weed abundance

Figure 5.10 shows the percentage of all possible quadrats at which target species were present by landuse class (species are listed alphabetically). For example, bittersweet was present at 9 of the 54 quadrats sampled in forest near mid-aged residential development, giving a frequency of 17%, and present at 5 of the 78 quadrats sampled in forest near pasture, giving a frequency of 6.5% (to 2 significant figures). It is not appropriate to show absolute numbers of observations because different numbers of transects were laid in forest adjoining each landuse. Five target species were never recorded within forest and are not shown. Chilean flame creeper, elderberry, blackberry, bittersweet and sycamore were the most often observed species. These were also most frequent for individual landuse classes, except mid-aged residential, where Darwin's barberry is the second most common weed and spindleberry the fifth with blackberry and sycamore less common.

The same five species were the most abundant in terms of total percentage cover observed at all quadrats (Figure 5.11). It is not appropriate to represent percentage cover data by landuse class because different numbers of transects were laid from each class.

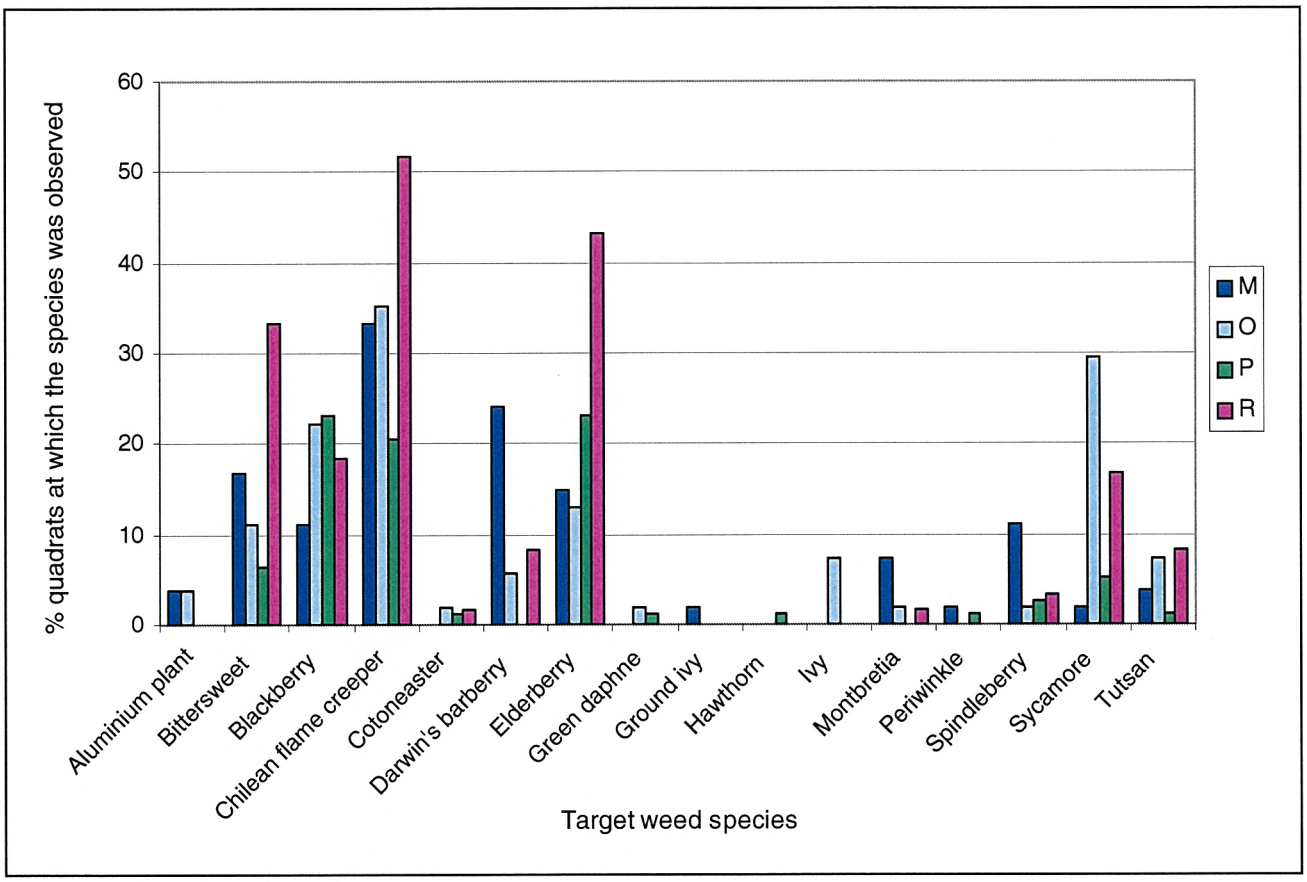


**Figure 5.10 Percentage of possible quadrats at which target weed species were observed by landuse class**

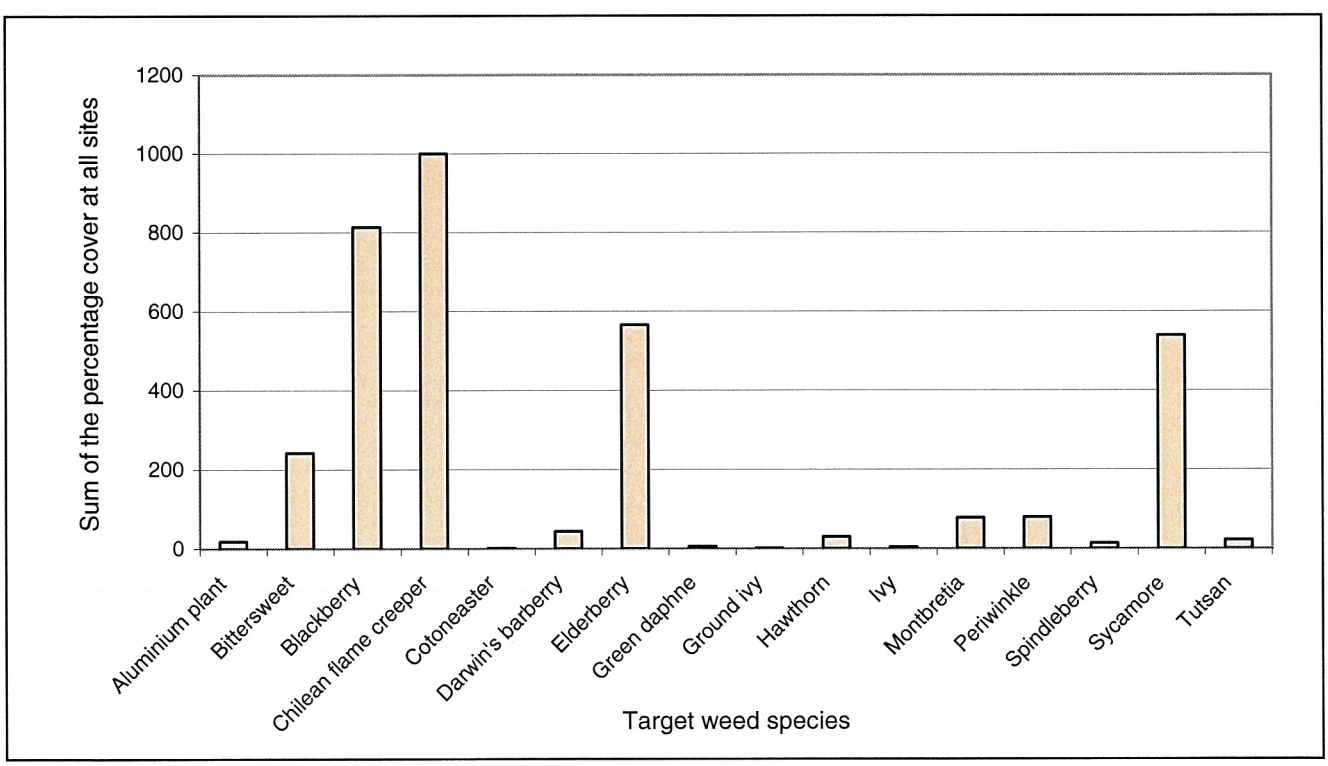


**Figure 5.11 Total percentage cover of target species at all sites**

## 5.4.2 Correlation of weed abundance and indicators of spatial context

This section presents outcomes of tests for correlations between weed abundance within forest remnants and characteristics of adjoining properties, the structure of the edge, and distance from the edge. Three possible linkages were proposed (shown in blue on Figure 2.10):

*8. Environmental weed abundance decreases with increasing distance from the forest edge.*

*9. Environmental weed abundance is negatively correlated with increased closure of edge structure.*

*11. Abundance of environmental weeds within forest is correlated to number of weed species in the nearby matrix.*

The overall research question can also be tested by this data, is stated as an hypothesis:

*Abundance of environmental weeds in forest patches is positively correlated with residential development in the matrix.*

There is little evidence to support the over-arching research question when phrased as a simple hypothesis (Table 5.10). Percentage cover of three weed species is positively correlated with age of adjacent housing, which supports the hypothesis. However, elderberry cover is significantly negatively correlated with house age, the reverse of the predicted outcome, and there is no significant correlation between any of the aggregate measures of weed abundance and the age of adjacent housing. In fact, most weeds are in forest close to recent residential properties (Figures 5.12 and 5.13).

The findings for Hypothesis 11 are ambiguous: percentage cover for three species is positively correlated with the number of weed species found on the adjacent property, indicating those weeds are more abundant close to weedier properties. Several species, such as montbretia and aluminium plant, were noted both in gardens and in adjacent forest where, considering the data in Table 3.1, they had presumably spread by human mediated dispersal from the nearby gardens. However, some species showed significant inverse correlations and significant correlation were not found with any aggregate measures of weed abundance.

**Table 5.10 Correlation of weed abundance with distance from the forest edge, characteristics of adjoining properties and edge structure.**

| | Distance from the edge | Age of adjacent development | Weediness of adjacent property | Edge structure |
|---|---|---|---|---|
| **Aluminium plant** | -0.020 | 0.118 | 0.050 | -0.005 |
| **Bittersweet** | -0.154* | 0.010 | -0.221** | -0.194* |
| **Blackberry** | -0.016 | -0.043 | 0.196** | 0.032 |
| **Chilean flame creeper** | -0.047 | 0.122 | 0.083 | -0.206** |
| **Cotoneaster** | 0.053 | -0.074 | 0.044 | -0.002 |
| **Darwin's barberry** | -0.073 | 0.139* | 0.078 | -0.224** |
| **Elderberry** | -0.034 | -0.127* | -0.199** | -0.038 |
| **Green daphne** | 0.027 | 0.019 | -0.022 | -0.002 |
| **Ground ivy** | -0.094 | 0.030 | 0.052 | -0.003 |
| **Hawthorn** | -0.019 | -0.077 | -0.038 | 0.072 |
| **Ivy** | -0.019 | 0.133* | 0.193** | -0.006 |
| **Montbretia** | -0.171** | 0.086 | 0.039 | 0.085 |
| **Periwinkle** | -0.133* | -0.039 | 0.043 | -0.055 |
| **Spindleberry** | -0.028 | 0.054 | 0.066 | -0.050 |
| **Sycamore** | 0.033 | 0.180** | 0.138** | 0.047 |
| **Tutsan** | 0.024 | 0.065 | 0.009 | -0.093 |
| **Total target spp. cover** | -0.128* | 0.066 | 0.056 | -0.099 |
| **Total number of target spp.** | -0.128* | 0.119 | 0.046 | -0.199** |
| **Total exotic spp. cover** | -0.224** | 0.027 | 0.019 | -0.101 |
| **Total number of exotic spp.** | -0.279** | 0.074 | 0.005 | -0.226** |

Entries are as in Table 5.6

In contrast, Hypothesis 8 seems acceptable. Three target weed species are significantly correlated with distance to the forest edge, as are all of the aggregate indicators of weed abundance. Significant correlations are negative, indicating that exotic plant cover and species diversity tend to decrease with increasing distance into the forest. Figures 5.12 and 5.13 show trends in the abundance of exotic species with distance to the edge.

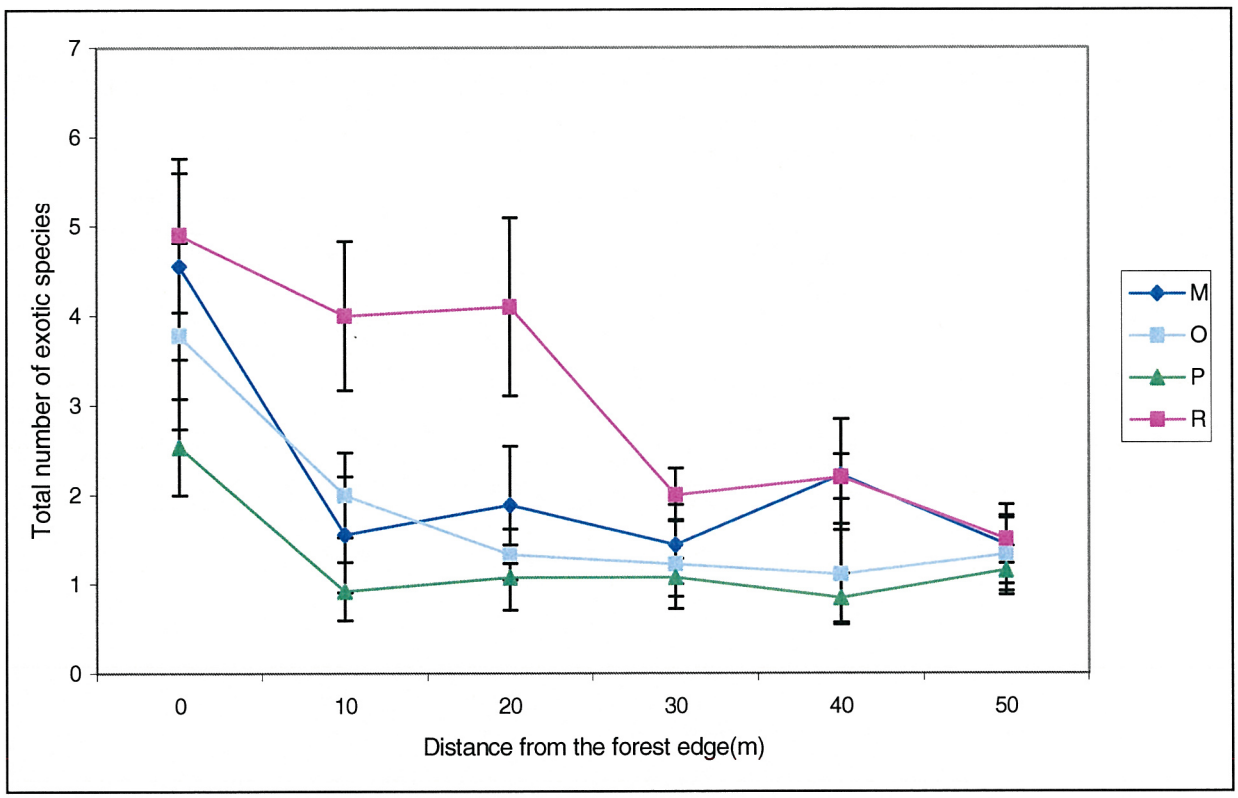


**Figure 5.12 Mean number of exotic species at a quadrat with distance from the forest edge by landuse class**

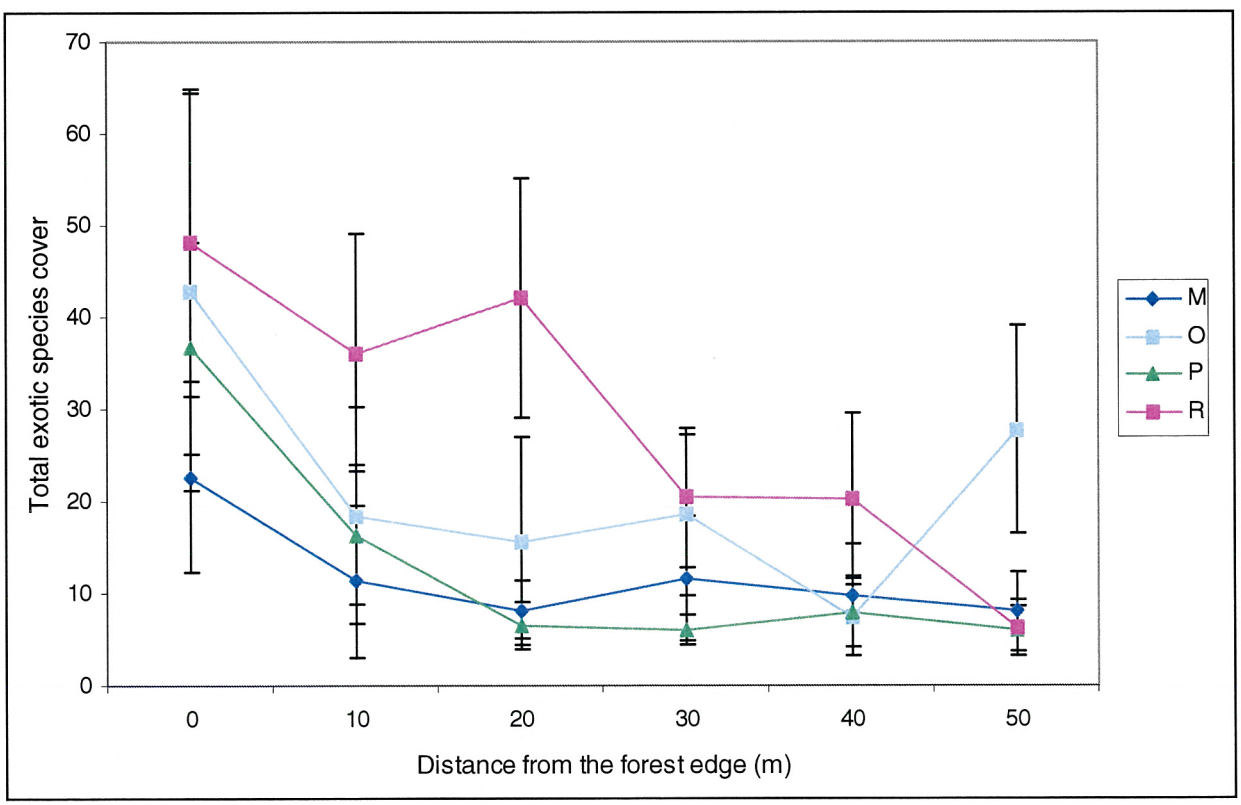


**Figure 5.13 Mean exotic species % cover at a quadrat with distance from the forest edge by landuse class**

Note: Bars show the standard error associated with each mean.

Hypothesis 9 is supported by the field data. Edge structure clearly influences weediness in the forest patch. There are negative correlations between the index of edge structure and numbers of (i) target species and (ii) all exotic species. This shows that as a forest edge becomes sealed by bushy vegetation, the diversity of weeds in the forest decreases. The cover of three target species was negatively correlated with increasing bushiness of edge structure, but measures of aggregate weed cover showed no such relationship.

A correlation between weed diversity and edge structure could reflect decreased propagule supply through more sealed edges, or effects of edge structure on light availability and disturbance ranking. The former is more likely to operate at Otatara because it would be expected that the latter would also cause raised weed biomass, as indicated by total percentage cover, which was not the case.

Five species were significantly more abundant, and all measures of aggregate weediness were significantly higher in forest adjacent to unfenced edges (Table 5.11), which supports Hypothesis 9. Edge fencing is important because it limits the entry of animals which can maintain an open edge structure, cause disturbance within the forest, and may disperse weed propagules.

**Table 5.11 Weed abundance and presence of fencing at the transect origin.**

| | Mean rank fenced | Mean rank unfenced | *U* value |
|---|---|---|---|
| **Aluminium plant** | 121.5 | 124.65 | 6840.0 |
| **Bittersweet** | 111.55 | 130.39 | 5944.5** |
| **Blackberry** | 120.34 | 125.32 | 6736.0 |
| **Chilean flame creeper** | 118.38 | 126.45 | 6559.5 |
| **Cotoneaster** | 123.36 | 122.79 | 6942.5 |
| **Darwin's barberry** | 117.17 | 127.15 | 6450.5* |
| **Elderberry** | 113.74 | 129.13 | 6142.0* |
| **Green daphne** | 123.86 | 123.29 | 6978.5 |
| **Ground ivy** | 123.00 | 123.79 | 6975.0 |
| **Hawthorn** | 124.37 | 123.00 | 6942.0 |
| **Ivy** | 121.50 | 124.65 | 6840.0 |
| **Montbretia** | 121.86 | 124.45 | 6872.5 |
| **Periwinkle** | 122.50 | 124.08 | 6930.0 |
| **Spindleberry** | 123.42 | 123.54 | 7013.0 |
| **Sycamore** | 113.41 | 129.32 | 6112.0** |
| **Tutsan** | 117.50 | 126.96 | 6480.0** |
| **Total target spp. cover** | 104.87 | 134.25 | 5343.0** |
| **Total number of target spp.** | 94.95 | 139.97 | 4450.5** |
| **Total exotic spp. cover** | 104.58 | 134.41 | 5317** |
| **Total number of exotic spp.** | 92.65 | 141.30 | 4243.5** |

Note: the right hand column gives the Mann-Whitney *U* statistic. ** significant at 0.01; * significant at 0.05 (2-tailed).

## 5.5 Characteristics of the forest environment and weed abundance

There are several plausible correlations between weed abundance and conditions within the forest (green links on Figure 2.1). Relevant hypotheses are:

1. *Environmental weed abundance is positively correlated with light availability.*

2. *Environmental weed abundance is positively correlated with concentrations of soil nutrients.*

3. *Environmental weed abundance is positively correlated with intensity of anthropogenic disturbance.*

Table 5.12 (overleaf) provides evidence that supports Hypothesis 1. The abundance of three target species, and the aggregate indicators of weediness, were significantly positively correlated to the amount of available light, indicating that better lit environments tend to support a greater abundance of weedy plants and a wider range of species. However, while significant, the rho values are small, indicating that the correlations are not strong, and one species, montbretia, appeared more abundant in shady conditions.

Hypothesis 3 was also supported by this data: percentage cover of four environmental weeds and all aggregate measure of weediness are significantly positively correlated with disturbance ranking. This implies that places with a higher disturbance ranking are likely to be weedier. Rho values are uniformly small.

**Table 5.12 Correlation of weed abundance with disturbance rank and light availability**

| | Disturbance rank | Light availability |
|---|---|---|
| **Aluminium plant** | 0.115 | -0.004 |
| **Bittersweet** | 0.186** | 0.193** |
| **Blackberry** | 0.057 | 0.235** |
| **Chilean flame creeper** | 0.106 | 0.256** |
| **Cotoneaster** | 0.023 | 0.030 |
| **Darwin's barberry** | 0.172* | 0.032 |
| **Elderberry** | 0.089 | 0.061 |
| **Green daphne** | -0.035 | 0.032 |
| **Ground ivy** | 0.098 | -0.108 |
| **Hawthorn** | -0.065 | . |
| **Ivy** | -0.05 | .001 |
| **Montbretia** | 0.159* | -0.135* |
| **Periwinkle** | 0.113 | 0.100 |
| **Spindleberry** | 0.054 | -0.084 |
| **Sycamore** | 0.009 | -0.081 |
| **Tutsan** | 0.128* | 0.106 |
| **Total target spp. cover** | 0.156* | 0.291** |
| **Total number of target spp.** | 0.253** | 0.274** |
| **Total exotic spp. cover** | 0.249** | 0.266** |
| **Total number of exotic spp.** | 0.392** | 0.264** |

Notes: entries represent Spearman's rho coefficient. ** significant at 0.01 (2-tailed); * significant at 0.05 (2-tailed).

Table 5.13 (overleaf) shows no support for Hypothesis 2. The percentage cover of Chilean flame creeper, tutsan and elderberry are significantly correlated to the concentrations of available nitrates, phosphates and magnesium, respectively but all correlations are negative, indicating that the species tend to be more abundant in environments where nutrient concentrations are low. All indicators of aggregate weediness are also negatively correlated with the concentrations of those nutrients. This suggests that soil nutrient status is not a limiting factor for plant growth at Otatara.

**Table 5.13 Correlation of weed abundance with soil nutrient concentration**

| | Nitrate | Ammonia | Phosphate | Potassium | Calcium | Magnesium | Soil pH |
|---|---|---|---|---|---|---|---|
| **Aluminium plant** | -0.060 | -0.090 | -0.076 | -0.118 | 0.005 | -0.046 | -0.038 |
| **Bittersweet** | -0.168 | -0.062 | -0.080 | -0.110 | -0.088 | -0.095 | -0.071 |
| **Blackberry** | -0.146 | 0.003 | -0.163 | -0.137 | -0.018 | -0.123 | -0.016 |
| **Chilean flame creeper** | -0.248* | -0.058 | -0.065 | 0.028 | -0.173 | -0.043 | 0.027 |
| **Cotoneaster** | -0.039 | 0.059 | 0.069 | 0.131 | 0.000 | -0.030 | -0.024 |
| **Darwin's barberry** | 0.027 | 0.026 | -0.038 | -0.040 | -0.019 | -0.067 | 0.033 |
| **Elderberry** | -0.052 | -0.079 | -0.092 | 0.081 | -0.082 | -0.226* | -0.113 |
| **Green daphne** | . | . | . | . | . | . | . |
| **Ground ivy** | . | . | . | . | . | . | . |
| **Hawthorn** | . | . | . | . | . | . | . |
| **Ivy** | . | . | . | . | . | . | . |
| **Montbretia** | -0.147 | -0.048 | -0.147 | -0.002 | -0.048 | -0.025 | -0.009 |
| **Periwinkle** | -0.106 | 0.061 | -0.011 | 0.115 | 0.029 | -0.038 | 0.063 |
| **Spindle-berry** | -0.030 | -0.155 | -0.142 | -0.074 | -0.102 | -0.044 | 0.000 |
| **Sycamore** | 0.088 | 0.77 | -0.131 | -0.092 | 0.101 | -0.152 | -0.335 ** |
| **Tutsan** | -0.147 | -0.215* | -0.270* | -0.083 | -0.131 | -0.121 | -0.047 |
| **Total target spp. cover** | -0.245* | 0.007 | -0.227* | -0.080 | -0.227* | -0.268* | -0.192 |
| **Total number of target spp.** | -0.247* | -0.125 | -0.285 ** | -0.089 | -0.0246 | -0.306 ** | -0.209 |
| **Total exotic spp. cover** | -0.255* | -0.002 | -0.228* | -0.080 | -0.208 | -0.219* | -0.177 |
| **Total number of exotic spp.** | -0.227* | -0.114 | -0.289 ** | -0.088 | -0.201 | -0.239* | -0.159 |

Note: entries give Spearman's rho coefficient. ** significant at 0.01 (2-tailed); * significant at 0.05 (2-tailed). Blank entries indicate that species did not occur in quadrats where soil was sampled.

### 5.5.1 Environmental weeds of particular interest

Some target species were involved in more significant correlations than others. Only nine species showed at least one very significant correlation. The five most abundant species all showed at least two significant correlations, suggesting that there may have been insufficient data to detect correlations involving less abundant species. However some, like ivy and tutsan, while not particularly abundant, were involved in several significant correlations. The distribution and abundance of the five most common species were examined using multiple regression analysis.

## 5.6 Multivariate models

Multivariate regression analysis was used to ascertain how much of the variation in weed abundance can be explained by models that incorporate characteristics of the matrix and the forest interior as explanatory variables. The following section will attempt to determine which of those factors is the most significant control of weediness in the sampled forest patches at Otatara.

The results of regression analysis are shown in Tables 5.14 and 5.15 (overleaf). Binary logistic regression created models that predicted the presence of a species or group of specieswith fair success. Most models correctly predicted over 75 % of cases. In the best case, 86% of sites were correctly classified for the presence of sycamore. In the worst case, only 64 % of sites were correctly classified for the presence of Chilean flame creeper. That is the same rate of success given by the simple assumption that Chilean flame creeper will never be present - the species was recorded at 84 of a possible 246 quadrats, approximately 34%.

Ordinary regression using log (percentage cover when present) of a particular species or group of plants, was not very successful. The best, involving log(percentage cover of sycamore when present), explained just 19 % of observed variation. Most explained less than ten percent.

**Table 5.14 Results of reverse stepwise binary logistic regression of the presence/absence of five common weed species, any target weed species, and any exotic species against environmental characteristics**

| Model of the presence of: | Age of adjacent housing[1] | Weeds on adjacent property[1] | Structure of the edge[1] | Presence of fencing[1] | Distance from the edge[1] | Available light[1] | Disturbance rank[1] | Overall effectiveness of model[2] |
|---|---|---|---|---|---|---|---|---|
| **Bittersweet** | Na[3] | -0.273 ** (0.097) | na | 1.234* (0.482) | -0.025* (0.011) | na | na | 82.2% |
| **Blackberry** | -0.023* (0.011) | 0.4085** (0.110) | na | 0.710 ns (0.418) | na | 0.033 ns (0.021) | na | 81.4% |
| **Chilean flame creeper** | na | na | -0.493** (0.166) | na | na | na | na | 63.8% |
| **Elder** | -0.036** (0.012) | na | na | 1.230** (0.388) | na | na | na | 76.9% |
| **Sycamore** | na | 0.302** (0.117) | 0.994** (0.313) | 2.731** (0.654) | na | na | na | 86.4% |
| **Any target species** | na | na | na | 1.085** (0.313) | na | na | na | 73.3% |
| **Any exotic species** | -0.030** (0.010) | 0.287** (0.103) | na | 1.488** (0.403) | na | 0.124* (0.054) | 0.444* (0.199) | 79.6% |

Notes: [1] Values of coefficients for that variable (β); standard error of β is in brackets below; ** Wald chi-square significant at 0.01; * significant at 0.05; ns not significant but still contributes to model. [2] Proportion of cases correctly predicted by the model. [3] the variable is omitted from the final model.

**Table 5.15 Results of reverse stepwise regression of the log(% cover when present) of five common environmental weeds, any target weed, and any exotic species.**

| Model of the log-abundance of: | Age of adjacent housing[1] | Weeds on adjacent property[1] | Structure of the edge[1] | Presence of fencing[1] | Distance from the edge[1] | Available light[1] | Disturbance rank[1] | Overall effectiveness of model[2] |
|---|---|---|---|---|---|---|---|---|
| **Bittersweet** | -0.01**<br>(0.003) | na[3] | na | na | na | na | na | 0.165<br>38 |
| **Blackberry** | na | na | na | na | na | 0.016 ns<br>(0.009) | na | 0.056<br>44 |
| **Chilean flame creeper** | na | na | na | na | na | na | na | na<br>80 |
| **Elder** | na | na | na | na | -0.007 ns<br>(0.062) | na | na | 0.050<br>51 |
| **Sycamore** | 0.0015**<br>(0.005) | -0.108ns<br>(0.055) | na | na | na | na | na | 0.187<br>30 |
| **Any of the target species** | na | na | na | -0.164ns<br>(0.087) | na | 0.013*<br>(0.005) | na | 0.04<br>162 |
| **Any exotic species** | na | na | na | -0.222**<br>(0.084) | 0.006**<br>(0.002) | na | na | 0.071<br>173 |

Notes: [1] Unstandardised coefficient (B); standard error of B is in brackets below; ** t value significant at 0.01 (two-tailed); * t value significant at 0.05 (two-tailed); ns not significant but still contributes to the model. [2] Adjusted $R^2$; number of samples used to create the model is below. [3] the variable is not included in the final model.

### 5.6.1 Binary logistic models of presence/absence

All environmental variables used in binary logistic regressions were involved in at least one final model. Of the forest condition variables, disturbance rank was involved in one model - predicting the presence of any exotic species - whereas light availability is related to the probability of blackberry being present, and of any exotic species being present. These findings confirm support for the hypotheses tested earlier but do not suggest that forest interior conditions are of overwhelming importance in determining whether weedy species are present.

Spatial context seems to be a more important predictor of weed presence. Age of adjacent housing has a negative coefficient in the three models in which it was a significant factor, indicating that weedy species are more likely to be present in forest near younger residential properties. This contradicts the overall hypothesis of the research, but because regression coefficients are very small, so the implied effect is of minor importance.

Weediness of adjacent properties showed a positive relationship with presence of blackberry, sycamore, and any exotic species, but a negative relationship with the presence of bittersweet. The hypothesised relationship finds support in these results, although not in the correlations discussed earlier (section 5.4.2).

Distance from the forest edge is significant in only one model (presence of bittersweet), and the regression coefficient is very small. Condition of the edge seems a more important factor. Edge structure is the only environmental variable significant in the model of flame creeper presence, and is in the model of sycamore presence, although in the latter case a more open edge (indicated by a lower value) is related to lower probability of sycamore being present, contrary to the prediction of Hypothesis 9.

The presence of fencing is significant most of the models and is the only significant variable in the model of presence of any target species. This variable was recoded for logistic regression, with fencing present as the normal case (0), so that when the case changes (to 1) fencing is not present. A positive regression coefficient shows that increased probability of weeds being present is related to the absence of fencing. Results may reflect the role of edge structure in limiting weed dispersal into forest by decreasing wind speed and restraining animal distribution vectors, including humans.

### 5.6.2 Ordinary regression of log(% cover when present)

Regression models of the log (%cover when present) of environmental weeds mostly involved few variables (Table 5.15). Given the poor overall effectiveness of these models, they seem unlikely to yield useful conclusions. However, some observations can be drawn from them. Disturbance ranking is not significant in any model, but light availability - correlated to disturbance ranking - is involved in two: it is positively related to the log abundance of blackberry and all target species.

The age of adjacent housing was involved in two models, showing a positive (though not significant) relationship with log (%cover when present) of sycamore and a negative relationship with log (%cover when present) of bittersweet. Weediness of the adjacent property was not a significant factor in any of the models.

Vegetation structure at the edge was not incorporated in any of the models, but the presence of fencing featured in the models of abundance of target species and of all exotic species, in both cases with a negative coefficient, indicating that when a fence is present weed abundance is likely to be smaller, which supports the conclusions from correlation analysis (Table 5.11).

### 5.6.3 Model testing

Regression is not an effective way to determine which of several explanatory variables best account for variation in a response variable when there is co-linearity between explanatory variables (McPherson, 2001). Bivariate correlation analysis found significant correlations between many of the environmental variables, which could explain in part why multivariate regression analysis did not clearly support research hypotheses.

The ordinary regression models were checked by examining (a) plots of residuals against predicted values, and (b) normality of the residuals. A random scatter of points in a plot of residuals against predicted values indicates that the model is of appropriate form for the data and a clear trend suggests that there is systematic variation in the data for which the model does not account (McPherson, 2001). A non-normal distribution of residuals indicates that the assumption of normally distributed response variables may be invalid (ibid).

Visual inspection of scatter plots of unstandardised residuals against predicted values showed few distinct trends, suggesting that there was little systematic variation that the models did not

account for. It should be noted, however, that this test could not be usefully applied to the regression equation of log (%cover when present of Chilean flame creeper), which was of the form y = c. Scatter plots of outcomes from models of log (%cover when present) of bittersweet and sycamore both showed that as predicted log (%cover) increased, so residuals became larger. McPherson (2001) suggests that this trend indicates that the data did not meet the assumption of variance requited for regression analysis.

Quantile-quantile plots of residuals showed approximately normal distributions, except that residuals from the regression of log (%cover when present) of blackberry, appeared to have a skewed distribution, indicating that the equation may be unreliable. The Kolmogorov-Smirnov test for differences from a normal distribution showed that residuals from the regression equations mostly had non-normal distributions. There were three exceptions: log (%cover when present of all exotic species), log (%cover when present) of bittersweet and log (%cover when present of sycamore) which were not significantly different from a normal distribution in contradiction to the residual vs. predicted plots discussed above.

Overall, problems were encountered in interpreting the equations created by ordinary regression. The results of logistic regression, which makes fewer assumptions about the distribution of error, are likely to be more reliable.

## 5.7 Summary

This chapter has presented the results of field research at Otatara, largely structured around hypothesis testing based on bivariate correlation analysis. Of the 16 hypotheses developed in the course of an extensive literature review, ten were supported and six were rejected. Figure 5.14 shows the hypotheses supported by statistically significant links between variables.

Residential development was not directly correlated to weediness. Neither was the number of weedy species growing on the property, it is not related to weed abundance within forest. However, edges close to residential properties are more likely to have an open structure, and to be unfenced (both conditions that are correlated to with increased weediness). Further, residential development is associated with a more disturbed and lighter forest environment (which, again, are correlated with increased weediness).

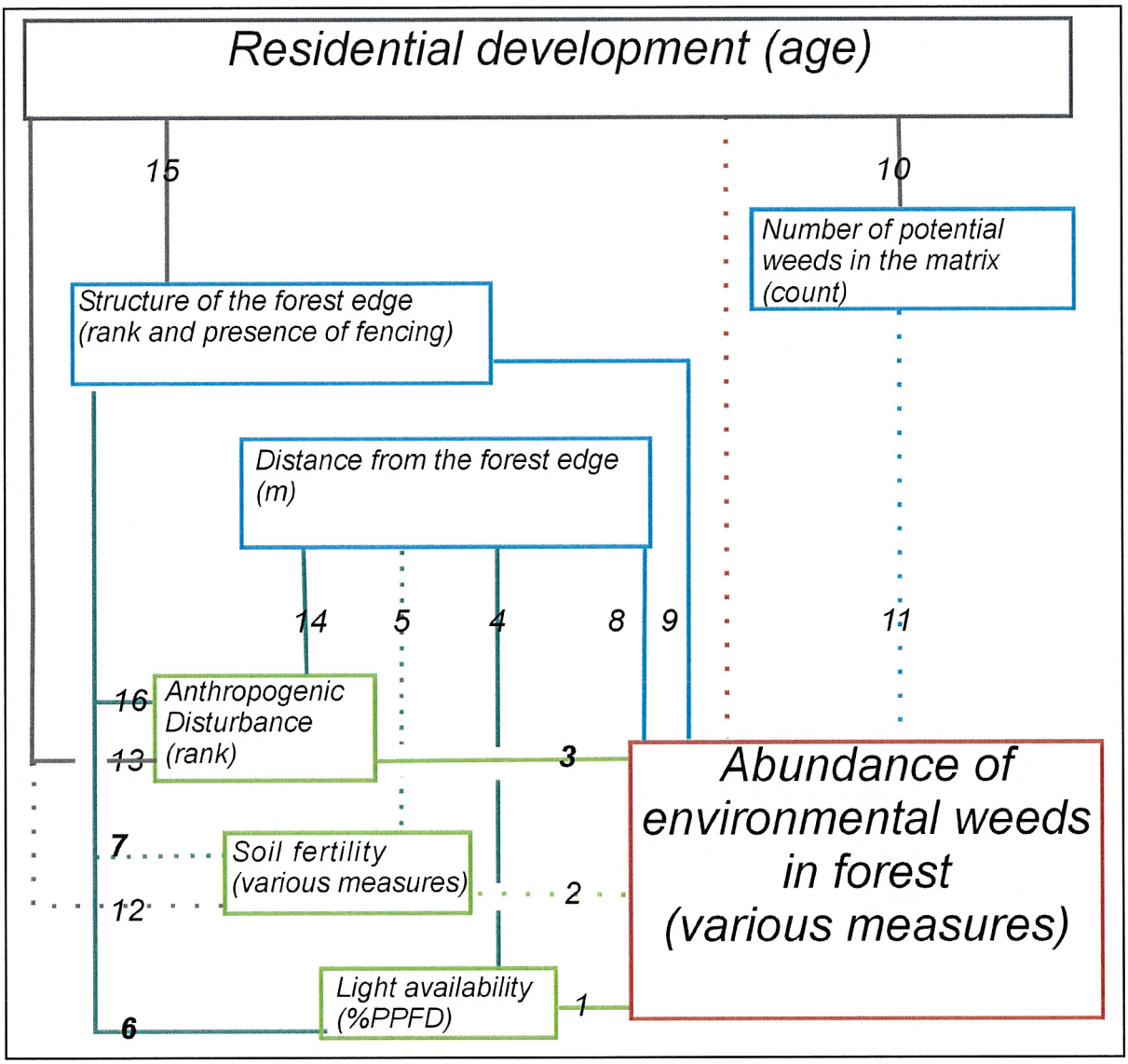


**Figure 5.14 Correlations between aspects of spatial context, conditions within the forest and weed abundance that appear to hold for Otatara (links shown as dotted lines were not supported).**

# Chapter 6

# Discussion

This chapter reviews the findings of research at Otatara and formulates a model of weed invasion in forest patches that is sensitive to land use changes in the matrix. The literature reviewed in Chapter 2 identified two requirements for successful habitat invasion by exotic plants: opportunities for dispersal into new habitat, and suitable conditions for establishment and growth within that habitat. It has been theorised that residential development may enhance opportunities for dispersal into forest - via fragmentation and the creation of edges, increased propagule supply, and enhanced transport mechanisms - and by altering environmental conditions within the forest to promote weed establishment.

This Chapter will explain the correlations described in Chapter 5 in terms of the theory of weed invasion. The linkages supported by data from Otatara (Figure 5.14) are used to create a conceptual model of weed invasion, which highlights the points at which residential development can enhance invasion success. There is evidence to conclude that the broad mechanisms identified in Chapter 2 operate at Otatara but there is no direct support for the overarching assertion that environmental weed abundance in forest is increased by residential development in the matrix.

This Chapter includes a discussion of methodological shortcomings that may explain why field observations do not support the overarching research hypothesis, particularly when other researchers have found contrary results a study from northern New Zealand is significant in this respect. Comparison of research findings from Otatara with those of other studies suggests that the relationship between weed abundance and residential development is more evident at some scales, and in some regions, than in others; it is geographically contingent.

# 6.1 A model of weed invasion

This section presents a general model developed from the concepts introduced in Chapter 2. The statistical results of Chapter 5 must be interpreted using a theoretical model because when many tests for bivariate correlations are performed on the one data set there is the risk that some correlations will be statistically significant merely by chance (McGarigal et al., 2000). A conceptual model is also an effective way of summarising the multiple potential effects of residential development.

## 6.1.1 Dispersal opportunities and weed abundance

The general model is outlined in Figure 6.1. It shows pathways that an exotic plant species may follow, resulting in either establishment as an environmental weed or failure to survive, as opposed to Figures 2.1 and 5.14 which show potential correlations between variables. The abundance of environmental weeds within a forest patch is determined by (1) the number of exotic plants introduced to the matrix close to the edge, and (2) whether or not conditions of the matrix allow those plants to grow and reproduce. Together, those determine the number of potential invaders. Which weeds may be present at a given point within the forest are controlled by (3), the structure of the forest edge and the amount of traffic through the forest edge, which determine the ease with which propagules move across the edge, and (4) the distance of the point of interest from the edge.

## 6.1.2 Effects of residential development

Residential development and the ensuing increase in human population density in the matrix alter opportunities for dispersal at all four control points, and so raise the abundance of environmental weeds within a forest patch. Residential properties host a larger pool of potential propagules because many more plants are introduced to residential areas, affecting control point (1), and there are more niches for plant growth in and around residential properties (2). In addition, residential properties tend to have open edges and give rise to an increased amount of human traffic into forest. Thus, more propagules penetrate the edge (3), and are transported deeper into the forest (4).

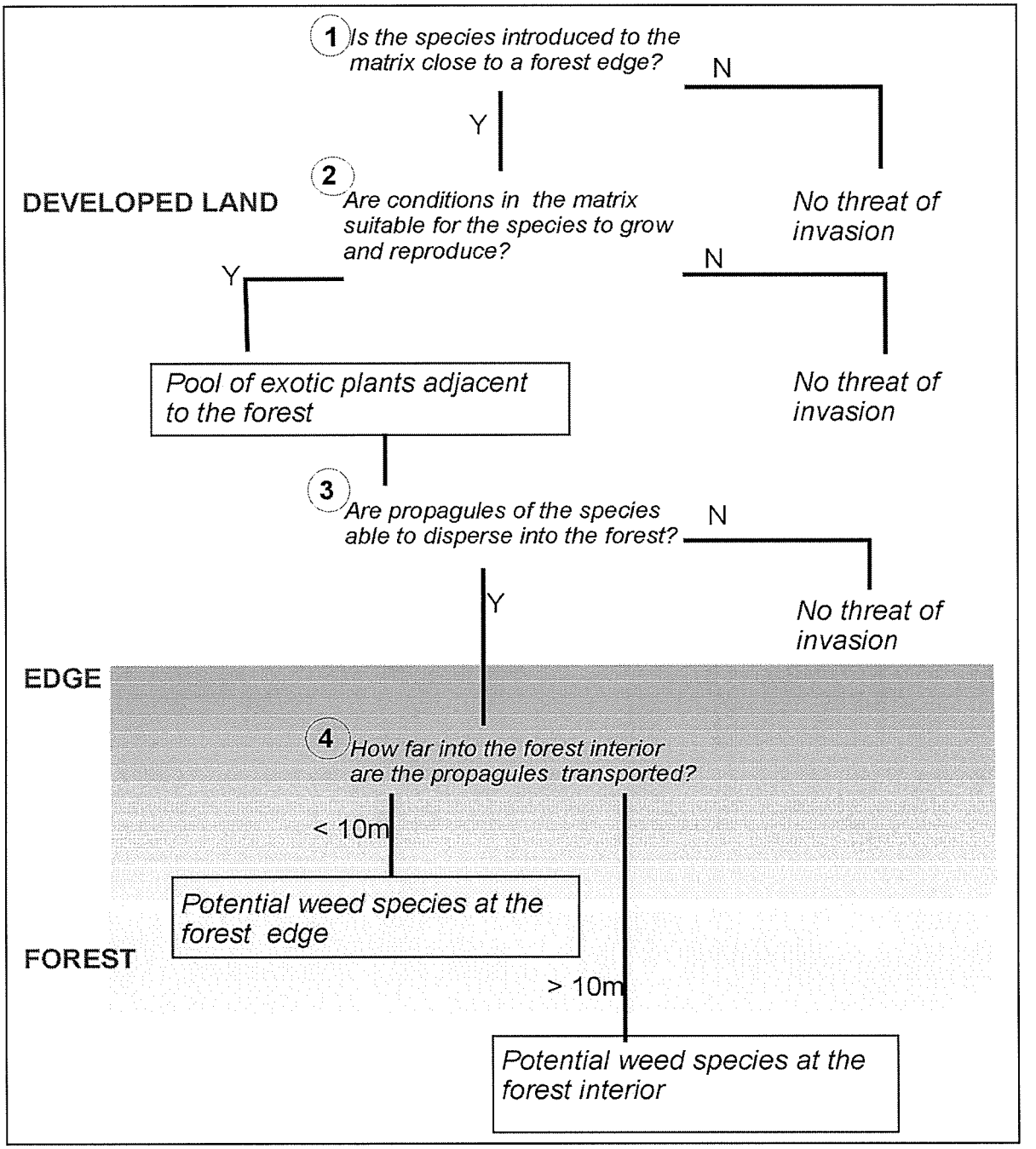


**Figure 6.1 General model of a weed spreading into forest, showing how dispersal influences weed distribution**

## 6.2 Model assumptions and predicted outcomes

The model incorporates several hypotheses relating to the overall research aim: to show how residential development changes the context of forest remnants and exacerbates weed invasion. It assumes that adjacent land uses should affect other aspects of spatial context, such as edge structure, and that those aspects of spatial context will, in turn, influence dispersal opportunities and weed abundance.

### 6.2.1 Effects of residential development on conditions at the forest edge

The model makes several critical assumptions about relationships between adjacent land use and aspects of spatial context. These assumptions complement hypotheses developed in Chapter 2, and were generally true of Otatara.

In accordance with points (1) and (2) in Section 6.1.1, there were more weed species on residential properties of greater age at Otatara. Such an association has been noted elsewhere. For example, Fensham and Cowie (1998) found that there was a positive relationship between time since establishment and number of naturalised plant species in and around settlements. Sullivan et al. (in prep.) examined the abundance of environmental weeds in coastal forest exposed to differing degrees of residential development in Northland. Their research is discussed below (Section 6.6). They found that the total number of exotic species observed in settlements, and the 'gardeniness' of settlements – being the average number of exotic plant species in the gardens of 10 houses per settlement – were positively correlated with estimated settlement age.

The effects of residential development at control points (3) and (4) were also evident at Otatara. Increased openness of edge structure is negatively correlated with increasing age of residential development on the adjoining property, and such properties are more likely to be unfenced. The model assumes that there will be more human traffic into the forest from residential properties than from other land uses and, because of this and the more open edge structure, greater numbers of exotic plant propagules will disperse further into the forest. Traffic into the forest was not specifically assessed at Otatara, but anthropogenic disturbance, which is related to this, tended to be more intense close to older residential properties

### 6.2.2 Effects of spatial context on weed abundance

The model assumes that the spatial context of forest in a matrix of developed land - such as characteristics of the adjacent property, structure of the forest edge, and distance from the edge – will, by influencing rates of dispersal, affect weed abundance within the forest. Again, those assumptions are associated with a cluster of hypotheses tested earlier (shown in blue on Figures 2.1 and 5.15).

One such assumption is that exotic plant species spread from the matrix into forest via edges, so there should be more environmental weeds close to a forest edge. This was clearly the

case for aggregate measures of weed abundance at Otatara, as elsewhere (Table 2.1). Such a pattern also occurs in the distribution of indigenous herbs colonising regenerating forest and is attributed to dispersal limitation (Singleton et al., 2001). It should be noted that dispersal rates were not directly quantified at Otatara.

The model also assumes that weed dispersal into forest will be enhanced where forest edges are unfenced or structurally open. Greater amounts of wind-dispersed seeds are likely to enter forest at open edges (Chapter 2). Open and unfenced edges are also more likely to be traversed by animal dispersal agents. There is indirect support for this assumption at Otatara: weed diversity (number of species) and the abundance of some individual species were significantly greater in forest with more open, and/or unfenced, edges.

The predicted outcomes of the model were not, however, observed at Otatara. The model proposes that there will be more weeds in forest adjacent to properties that host more known weed species, which was not true at Otatara. More importantly, the overarching hypothesis was not directly supported. There is no evidence that abundance of environmental weeds within a forest patch is correlated to the age of adjoining residential development. Following sections will discuss why predicted outcomes were not observed, although the mechanisms whereby residential development is proposed to increase weed abundance do appear to operate at Otarara.

## 6.3 Observations do not meet model predictions

There are two possible sets of reasons why predictions of the model (Figure 6.1) are not evident at Otatara. The first concerns limitations of the model itself: it does not allow that the relative importance of dispersal-related or environmental controls on the distribution and abundance of weed species may change over time. Considering this, the model can be refined to take into account other factors, particularly environmental characteristics of the forest, which may distort its predictions, especially when dispersal opportunity is not a limiting factor. The second concerns methodological shortcomings in data collection and/or analysis.

### 6.3.1 Failure to account for changing controls of weed invasion

The model in Figure 6.1 relates weed abundance in a forest patch to the presence or intensity of residential development in the matrix. It shows four points at which residential development may cause increased weed abundance by enhancing dispersal opportunities, but it does not incorporate the other requirement of successful invasion - availability of sites suitable for growth (Chapter 2).

Model predictions would be less clear if most environmental weeds have spread into all sites that are favourable for their growth and are not limited by the location of propagule sources or opportunities for dispersal into forest. As noted in Chapter 3, the research design used in this thesis implicitly assumes that the same suite of factors control weed distribution and abundance at every point in time. In fact, it is probable that dispersal opportunities control weed distribution during early stages of invasion, and suitability of habitat for establishment and growth will control distribution at later stages, as found by Wiser et al. (1998). Singleton et al. (2001) found that species that were significantly more common in old growth forest than in regenerating stands tended to be ant-dispersed, whereas species that were equally common in both environments were dispersed by birds or wind.

The following are situations in which it is probable that environmental weeds have spread into all sites favourable for their growth:

i) Plants were introduced in large numbers over a wide area.
ii) Plants were introduced many generations ago.
iii) Plants have a very effective means of dispersal.

## 6.4 Refining the conceptual model

The model can be revised to incorporate the second necessary condition for plant establishment: suitable sites for establishment and growth. The revised model thus incorporates recruitment as well as dispersal limitation. The former being a factor of known importance in controlling plant colonisation of regenerating forest by indigenous herbs (Verheyen and Hermy, 2001) as well as weed invasion (Chapter 2). The pattern of site availability may depend on natural variation, or be related to the spatial context of habitat and influenced by landuse in the matrix. The model outlined in Figure 6.2 provides for this. The

four control points proposed in the first model are still present, but are supplemented by three more that account for the process a potential weed establishing and spreading within the forest.

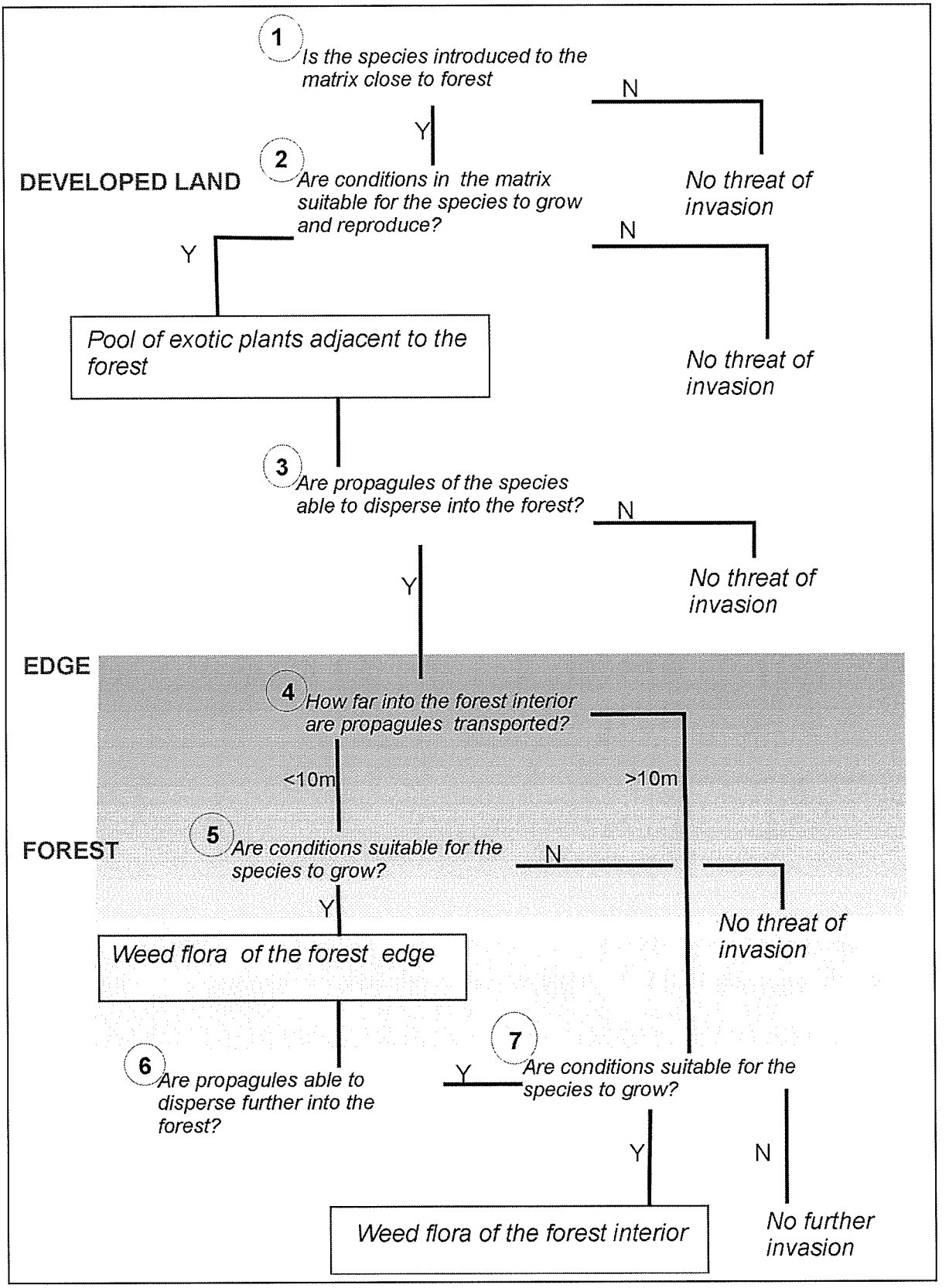


**Figure 6.2 Revised general model showing how dispersal and recruitment opportunities influence weed distributions**

### 6.4.1 Effects of residential development

Again, each control is influenced by land use in the matrix. For points 1-4 there is no change in the processes described above. It should be noted, however, that if weed distributions are not limited by dispersal then the importance of those points, particularly (1) and (2), will be reduced.

Control points (5), (6) and (7) depend on conditions within the forest. Controls (5) and (7) depend on the availability of resources necessary for a potential environmental weed to germinate and grow. Three factors which have been identified as controls over weed abundance in forest environment were assessed at Otatara: light availability, soil fertility and disturbance. Residential development - and resulting changes in edge structure - is proposed to alter these conditions in ways that facilitate invasion; that is, by increasing the amount of available light, increasing soil fertility, and increasing the amount of anthropogenic disturbance. However, these conditions are also subject to variations that could obscure the predicted effects of development.

Control (6) may be affected by residential development in similar ways to control points (3) and (4); that is, a more open edge will increase the chance propagules being transported deeper into the forest by wind, animals and (in conjunction with the raised local population density) people.

Thus, the augmented model makes assumptions about the relationship between weed abundance and environmental conditions within the forest, and how those conditions will be altered by residential development. Again, those assumptions parallel clusters of hypotheses tested earlier. The extent to which these assumptions hold at Otatara is discussed below.

### 6.4.2 Effects of forest interior conditions on weed abundance

The significance of habitat conditions in controlling the abundance of environmental weed species has been studied extensively. Overall, it seems that environmental weeds are most abundant in sites that offer ample resources for growth, such as water, light and soil nutrients (Chapter 2).

Ewel et al. (1999) proposed that: "humans alter land in ways that favour humans; species that do well in human-altered habitat in one area may be more likely to do so in another" (p 622). This statement is true at the broad scale. For example, pasture and hedge plants from Europe

thrive in New Zealand because people have disturbed indigenous habitats to replicate conditions under which those species became established in their natural ranges (Atkinson and Cameron, 1993). It can also be applied at a local scale: exotic plant species that do well in human-altered land - such as the matrix - are likely to do well in those parts of the forest where conditions most resemble those of the matrix; that is, where there is a history of anthropogenic disturbance, light levels are higher and the soil more fertile.

This assumption was represented in the cluster of hypotheses shown as green links in Figures 2.1 and 5.15. It was partially confirmed by data from Otatara, where weed abundance was positively correlated to disturbance ranking and light availability.

Environmental weed abundance was not positively correlated to soil nutrient availability. It should be noted that the hypothesis that artificial fertilisation enhances weed invasion derives from research in Australia where soils are often nutrient poor (for example, Clements, 1983), whereas Otatara soils are moderately fertile (Chapter 5) so nutrient supply may not be a limiting factor for plant growth.

### 6.4.3 Effects of the matrix on the forest interior

The revised model assumes that environmental weed abundance may be influenced by spatial context, even when dispersal opportunities are not limiting, because environmental conditions within the forest are altered by spatial context. This assumption embodies the cluster of hypotheses shown in sea-green and black in Figures 2.1 and 5.15.

Habitat conditions that resemble those of the matrix, and that favour the growth of exotic plants, often occur at the edges of a forest patch because those areas are most exposed to and influenced by matrix conditions (Saunders, 1991). This was the case with regard to anthropogenic disturbance in forest at Otatara, but not with regard to other forest environmental conditions.

Forest conditions were, however, sensitive to land use in the matrix and the condition of the forest edge. Both anthropogenic disturbance and light availability were found to be higher in forest near older residential properties, and to be positively correlated with increased openness of edge structure and the absence of fencing.

Soil fertility at Otatara is not sensitive to any of the measured aspects of spatial context, in contrast to studies that found relationships between soil fertility and urban development.

Such studies have been conducted in nutrient poor areas and in open woodland vegetation (Fensham and Cowie, 1998; Rose and Fairweather, 1997), so the different results from the thick forest at Otarara are not surprising. No relationship was found between soil fertility and environmental weed abundance, so the lack of correlation between soil fertility and social context is unimportant in terms of the model.

In summary, there is empirical support from Otatara for the revised model: residential development impacts upon forest environmental characteristics in ways likely to raise weed abundance. There was, however, no evidence to suggest that any of the forest habitat characteristics quantified in this study is an overriding control of weed distribution so mush so as to obscure the effects of residential development. Thus, the fundamental failure of the model stands: even though weed abundance is correlated to conditions in the forest interior and to aspects of spatial context, which are altered by residential development in ways that should increase weed abundance, no correlation between weed abundance and residential development was found at Otatara

## 6.5 Methodological shortcomings

It might not be possible to demonstrate a relationship between age or weediness of adjacent development and weediness within the forest at Otatara because the distribution of weeds in the forest is not controlled by dispersal from nearby sources of propagules. Yet weed abundance at Otatara is correlated to distance from the forest edge, and it is generally assumed that if plant abundance is related to distance from a source of propagules, then dispersal limitation is a partial control of their distribution (Harrison et al., 2001; Jesson et al., 2000; Singleton et al., 2001; Verheyen and Hermy, 2001). It is, however, important to acknowledge "pattern does not imply process" (Lawton, 1999), an observed distribution could result from several possible mechanisms. There are many potential reasons that forest edges are weedier than the forest interior at Otarara.

Firstly, the pattern may be an outcome of environmental edge effects rather than of dispersal limitations. This possibility has already been examined in the discussion of the importance of control points (5), (6) and (7). While there was some evidence that those controls relating to establishment opportunities are important, it seems unlikely that they are the only cause of an edge related distribution. Anthropogenic disturbance was the only forest interior variable to show a significant gradient from edge to interior. It may be that this trend is the only cause of

the negative correlation between weed abundance and distance from the forest edge, and that there is no link between residential development and weed abundance in nearby forest.

Alternatively, problems in data collection or overall research design could explain why an edge related weed distribution was observed in the forest, but the expected correlation between overall weed abundance and residential development was not found. It may be that an environmental characteristic of the forest or its spatial context (that is, one of the eight boxed elements in Figure 2.1) may have been measured inaccurately, or that an important control factor was overlooked. It is also possible that the study was conducted at too small a scale for it to distinguish direct correlations between land use in the matrix and weediness within forest. These possibilities are discussed below.

### 6.5.1 Possible sources of error in assessing spatial context

Errors in the quantification of environmental characteristics may explain why the expected relationship between residential weed abundance was not found by statistical analysis. The methods described in Chapter 4 will be briefly re-examined to see if such shortcomings are likely.

The measures used to describe the structure of the edge and distance in from the edge were simple, robust and widely used. In some cases a transect may have been influenced by an edge other than that of the origin. Care was taken in laying out transects to ensure that every quadrat was closer to the edge at the origin than to any other edge, but this was not always possible because of the small size and irregular shapes of some forest patches (refer to Figures 5.1-5.8). A transect length of 50m was assumed sufficient to penetrate to the forest interior, so that measurements of abiotic conditions (principally light) would capture the gradient from edge to interior. Edge effects could be especially severe at Otatara, where strong winds are common (Norton, 1996), so this assumption may be untenable. However, an edge related trend in weed abundance was detected. Logically, if light availability or soil fertility were responsible then they would also show an edge related pattern.

It is more likely that the measures used as descriptors of the matrix - age of the nearest house, and number of known weeds growing on the nearest property - were inappropriate. This is not because they were inaccurately measured, although it is possible that landowners may have been incorrect in their estimate of the initial date of house construction or that target weeds were overlooked. Rather these variables are problematical because they are limited surrogates for a complex set of factors.

It seemed reasonable to assume that the effects of development will be greater in places where development has been in place for longer periods than in places with a shorter history of development. Other studies have found significant relationships by using age as a surrogate for degree of development (section 2.4), and some theorised effects of development - the potential weed pool near the forest edge and anthropogenic disturbance - were positively correlated to age of development at Otatara.

Even though there was no significant correlation between the age of residential development and weed abundance on adjacent properties, there tended to be more weeds in forest near residential properties of any age than there were in forest adjoining pasture. Weeds were often most abundant near recent residential developments. Forest was not much less disturbed at those sites than at old residential sites (Figure 5.9), and the forest edge was more open. Both those factors are positively correlated with weed abundance, so it may be that the initial disturbance - particularly changes to edge structure - associated with housing construction significantly alter weed abundance within the forest, but this effect will not continue to operate over the entire history of residence. Thus, stronger correlations might have been evident had the research been structured as a binary comparison between forest adjoining residential properties and forest adjoining pasture.

### 6.5.2 Possible sources of error in assessing forest environments

There may have been methodological problems in the collection and/or analysis of data to describe the forest interior. The accuracy of the methods used to quantify light availability and soil fertility can be assessed by comparing the research results to those of similar studies.

McDonald and Norton (1992) reported values for autumn recordings of %PPFD in two podocarp forests on the West Coast, with ranges of 0.9 to 6.69 and 1.1 to 8.1, respectively. These values are comparable to mean available light at Otatara, although the range there is much greater. This may be because McDonald and Norton measured PPFD over a whole day, instead of over a twenty-minute period, but the data collected at Otatara seem reasonably accurate.

It has been suggested that measurements of light intensity should capture seasonal variation. If not, relationships between light availability and vegetation may be obscured (Wilson and Tilman, 1993). Brothers and Spingarn (1992) suggested that their inability to find a correlation between exotic species abundance and light availability was due to the short

period over which incident light levels were measured. Data collection at Otatara did not capture seasonal variations in light, and that may be why an edge effect was not detected, although the expected positive correlation with weed abundance was observed.

Concentrations of soil nutrients measured in the present study are not very different from standard values for the Otatara yellow-brown sand (DSIR 1968), which suggests that there were no significant errors in measurement. The standard values reported for the A(ii) horizon under totara forest in this area are similar to the mean values found in the present analysis (given in brackets): standard values for Ca, Mg, and K were 8.6 (10.8), 5.6 (3.8), and 0.5 (0.4) me/100g, respectively, and the standard for troug-extractable phosphate was 20 (38) ppm. No general values were reported for available nitrogen, so the measures of nitrates and ammonium cannot be checked against a published reference. As was the case for light availability, while the means found in this study are comparable to those determined by other researchers, variance was large.

Soil fertility seems unlikely to be a limiting factor for weed growth at Otatara, given that nutrient availability is generally average to high. Blakemore et al. report that, "New Zealand soils display considerable nutrient enrichment of their topsoils due to the effects of the active organic cycle under forest... " (1987 p 102), which supports this conclusion. It is possible that the concentration of a neglected trace element explains weed distribution, but the *General Survey* of South Island soils does not mention such a lack in Otatara soils (DSIR, 1968).

All hypothesised relationships involving disturbance ranking are supported by data collected at Otatara. This seems to indicate that the measurement system was appropriate, although observer bias cannot be ruled out.

There are several potential sources of error in the quantification of weed abundance. Incorrect species identification is unlikely because a limited set of species was considered, and sample plants were taken for taxonomic identification when there was uncertainty. The disadvantage of this strategy was to underestimate the total number of exotic species (Chapter 4). This was a potential source of error but only for that one measure.

Estimates of plant abundance represent a snapshot at one point in time. Measurements were taken in spring, which may have introduced error in the estimation of total percentage cover, as some species had probably not reached their maximum biomass for the year. In the case of Chilean flame creeper, its presence may also have been underestimated because it dies back completely in winter. However, dead stems are usually obvious.

Some significant characteristic of the forest interior, which is a key factor controlling weed distribution, may have been overlooked. There were no obvious differences in topography or hydrology in the Otatara landscape, but there were differences in forest composition (Section 5.1).

The potential effects of diversity or competition of the invaded community are often outweighed by other factors (Chapter 2), but this is a recurring theme in the literature and may be a controlling factor at Otatara. This research has not examined the effects on competition of the extant vegetation, or the effects of a new species colonising a forest patch, which is widely predicted to result in loss of indigenous biodiversity (Chapter 1). Further research that quantifies indigenous and exotic species abundance should contribute to a better understanding of the role of competition in the weed invasion process.

Another factor that was not accurately assessed, and that has serious implications for weed abundance, is weed control. From conversation with residents it seems that at least 15 of the 29 properties visited in this research were subject to some weed control by private landholders. Seven of the 15 private landholders mentioned that their efforts were confined to the forest close to their gardens and driveways, which would distort patterns of distribution. A few weed species were mentioned. These were chiefly abundant species, such as *Muehlenbeckia*, blackberry, flame creeper and elder. Some of the transects were in public reserves, where the ICC and Landcare Group undertake weed control (Chapter 3).

Other aspects of the history of the indigenous forest at Otatara were not considered. Forest patches at Otatara have been extensively modified (Chapter 3). Selective logging may have allowed edge effects to penetrate more further into the forest (Fraver, 1994) and would have created pathways and nodes of disturbance in the forest. These effects would aid weed dispersal and establishment. The observed environmental weed distributions may, therefore, owe as much to past patterns of disturbance within the forest as to the presence of housing at the edge. Chilean flame creeper illustrates the importance of previous disturbance in controlling present distribution. Although present in forest for some time, this species, which is thought to require high light levels for germination, was originally confined to canopy gaps and edges. It only became a widespread environmental weed after severe frost in 1996 thinned the canopy and allowed it to establish in the interior (West, 2001).

### 6.5.3 Problems of scale

Scale is an important component of landscape ecological research because different phenomena are evident at particular scales (Pickett and Cadenasso, 1995). A potential explanation for the lack of clear correlation between characteristics of the matrix and weediness of forest patches in the present study may be that this research was conducted over an area too small for patterns of weed distribution to be detected, especially if weed propagules can spread easily through the matrix or have had ample time for dispersal.

Dispersal of exotic propagules in the matrix is likely to be more effective than within forest because winds are stronger, there is more human traffic, and exotic animals, such as frugivorous birds, are common. It is unlikely that all the propagules reaching the forest at an edge originate from the property adjoining the edge at that point. This implies that the effects of controls (1) and (2) in the proposed model may be unimportant at the scale of this research. Even though propagules reach the edge with relative ease, dispersal into and through the forest may still be limited, that is, controls (3) and (4) could still be effective, explaining why an edge related distribution was observed.

Because weeds may disperse readily throughout the matrix of residential and agricultural land, it may have been more appropriate to characterise the matrix in the wider vicinity of the transect, or entire forest patch, than at one property. For instance, Magee et al. (1999) categorised the matrix in terms of the predominant land use in a 100m radius of each wetland patch they measured (refer also to Sullivan et al.'s work, discussed below). This approach would have captured most of the potential sources of weed propagules (Figure 4.1) but did not allow them to identify which dispersal routes into forest were most significant.

The research conducted here searched for a correlation that would indicate the importance of one potential dispersal route into the forest – spread from a population on the nearest cleared land - and that pathway seems to be relatively unimportant at Otatara. This is reasonable, as many of the target weed species have a long history of naturalisation, so propagules are as likely to be sourced from wild populations on waste ground, road sides, hedges and so on than from gardens (Figure 4.1).

Otatara is a small area, and all study sites were within a few kilometres of each other. Often houses of different ages are juxtaposed. Description of the matrix at a broader scale, one that captured more of the potential source-region or catchment for propagules at each study site, would probably have shown it to be homogenous. This suggests that Otatara may not be the

perfect location for such research. The ideal location would contain a number of forest patches of equal area. Each forest edge would neighbour only houses in one age class and the study sites would be a considerable distance apart. Such an area could only be found by selecting sites that were in different ecological districts or regions, at cost to the homogeneity of other environmental characteristics such as substrate and forest type.

Most studies that have detected a relationship between development and weed abundance followed the line advocated by Lawton (1999); that is, to search for general patterns that may be codified into laws at landscape or regional scales. However, those studies do not include much information about the role of local environmental characteristics (Batianoff and Franks, 1998; Fensham and Cowie, 1998; Timmins and Williams, 1991).

## 6.6 Comparison of Northland and Otatara

Sullivan et al. (in prep.) conducted their research in coastal forest reserves in eastern Northland. As noted above, the two key predicted outcomes of the model of weed invasion and residential development that were not supported by data collected in Otatara were upheld by their findings. It is revealing to contrast the studies.

Both were conducted in coastal areas close to cities, and development in both areas has long been associated with holiday homes and 'lifestyle' properties. Otatara is the smaller settlement, adjacent to Invercargill and has experienced very slow population growth in the past decade. The Northland Study was based in the area around Whangarei, which is slightly smaller than Invercargill (population 41500) but expanding (Whangarei Online, 2001).

### 6.6.1 Differences in research design and methods

The principle difference between the two research designs is the scale of investigation. Sullivan et al. (in prep.) considered the relationship between total number of exotic plants within forest reserves and characteristics of the nearby 'settlement'. In contrast, the present study attempted to correlate conditions along 50m transects into the forest with characteristics of a single property (that at the origin). This design assumed that all points along a transect are influenced only by the land use at the transect origin which, as discussed above, may not be a reasonable assumption.

The following example illustrates a shortcoming of this research design: Otatara Scenic Reserve is bordered on its northern side by old residential properties, several of which support mature sycamore trees. The presence of these trees was only noted in analysis of transects which originated from properties where they grew – in which case they would raise the score of 'weediness of adjacent property'. Transects which originated from a few houses down, or even on the other side of the reserve, might experience increased seed rain because of the presence of those trees, but that was not recorded in the 'weediness of adjacent property score'.

Sullivan et al. used a broader set of characteristics to define the matrix, particularly in terms of the relative extent of development. They described the surrounding matrix by number of houses within 250m of the forest reserve, age of the oldest house, and density of housing within 500m and 1km of the reserve. The source catchment of potential environmental weeds was characterised in terms of the total number of exotic plant species observed in each settlement (including non –gardened areas) and the number of exotic plant species present in a sampled 10 gardens from each settlement. This captured more of the possible routes of dispersal into the forest (Figure 4.2).

Those differences, particularly scale, may explain why the key model predictions were evident in Northland but not at Otatara. However, no information was collected about residential development and conditions at the forest edge or in the interior, or the correlation of weed abundance with those factors. The detail of the findings presented here is an advantage of the small-scale research design employed.

## 6.6.2 Differences in the weed flora

Differences in weed flora between the two areas may also explain why weediness in forest patches in Northland was more strongly correlated to the weediness of nearby residential development than was the case in Otatara.

The difficulties of defining a weed were discussed earlier. It has been noted that the Northland study used a more general definition, but it was considered appropriate to focus on known environmental weeds at Otatara. Section 3.4.1 discussed whether intrinsic characteristics of an exotic species determine its pest status, and concluded that while some characteristics are shared by many weedy species, their status as weeds also depends on qualities of the invaded community. It follows that weeds have a geographic component: plants can be serious weeds in one locale and yet innocuous in another. For instance, several

ornamental exotic species are environmental weeds in southern Florida but not in the north (Ewel et al., 1999). That suggests the likelihood of differences in the weed floras of Northland and Otatara.

As discussed above, the predictions of the model may be distorted if weed species are not limited by dispersal. Then, the role of residential development as a source of propagules will be relatively unimportant. It might be that the distribution of environmental weeds at Otatara does not reflect this role because its adventive flora is dominated by species that are not dispersal limited, while the Northland weed flora could include more species that are limited by opportunities for dispersal, and thus show a stronger relationship to residential areas as sources of propagules and of anthropogenic dispersal paths.

To test those hypotheses, the two floras were compared. "Flora" is defined as the set of species that were both (i) encountered within the forest at each location and (ii) in the relevant RPMS (this being an attempt to minimise differences between the definitions employed in the two studies).

The eastern Northland flora consisted of 25 species, the Otatara flora of 14, and 2 species were occurred in both (the latter are not included in the following comparison). The characteristics examined were growth form, the principle means of dispersal (where there are several means of dispersal, the most common is given. If that is not known, the most effective is given following the sequence birds> wind> water> gravity > vegetative) and the date of naturalisation in New Zealand (data sources in Appendix A).

**Table 6.1 Mean and range of dates of initial naturalisation of environmental weeds of eastern Northland and Otatara.**

| Date of first naturalisation | Eastern Northland | Otatara |
|---|---|---|
| Earliest | 1867 | 1867 |
| Average | 1932 | 1916 |
| Most recent | 1988 | 1988 |

Table 6.1 was created from data describing the first date that each species was recorded as naturalised anywhere in New Zealand, rather than specifically in Northland or Otatara. It is a general indication of how long a species has been an environmental weed. The species from Otatara tend to have slightly earlier dates of naturalisation, suggesting that they have had more time to spread from initial sites of introduction.

The eastern Northland flora is the more diverse (Table 6.2) Environmental weeds at Otatara were nearly all woody plants or vines, whereas there were more broadleaf herbs and a grass in eastern Northland

**Table 6.2 Environmental weeds in eastern Northland and Otatara by growth form.**

| Growth form | Eastern Northland | | Otatara | |
|---|---|---|---|---|
| Grass | 1 | 4% | 0 | 0 |
| Herb | 7 | 28% | 2 | 14.3% |
| Shrub | 6 | 24% | 3 | 21.4% |
| Small tree | 3 | 12% | 4 | 28.6% |
| Tree | 1 | 4% | 1 | 7.1% |
| Vine | 7 | 28% | 4 | 28.6% |
| Total | 25 | 100% | 14 | 100% |

The eastern Northland flora is also more diverse in terms of dispersal modes. Environmental weeds at Otatara are predominantly bird dispersed, which suggests that they are less likely to show simple dispersal limitation –Thomson (2000) found that woody weeds present in the interior of Southland forest remnants were all bird dispersed - while those at Northland are dispersed by a diversity of means including a higher percentage of vegetative, explosive or gravity dispersal, so that dispersal limited distributions are more likely.

**Table 6.3 Environmental weed species in eastern Northland and Otatara by dispersal mode**

| Dispersal mode | Eastern Northland | | Otatara | |
|---|---|---|---|---|
| Birds | 10 | 40% | 11 | 78.6% |
| Wind | 4 | 16% | 1 | 7.1% |
| Explosive | 1 | 4% | 0 | |
| Gravity | 2 | 8% | 0 | |
| Vegetative | 4 | 16% | 2 | 14.3% |
| Uncertain | 4 | 16% | 0 | |
| Total | 25 | 100% | 14 | 100% |

The definition of weediness - number of exotic species present - used by Sullivan et al. (in prep.) was different to that used in Otatara. They may have found stronger correlations

between this measure and the age and weediness of nearby settlements because their study was specifically designed to include garden escapes that are not widespread, whereas such plants were not targeted in the present study.

### 6.6.3 Weeds at Otatara

The target weed species at Otatara tend to be bird dispersed and to have a relatively long history of naturalisation, suggesting distributions no longer related to initial introduction sites, which is an important factor to be considered in trying to explain presence and abundance. Examination of forest herb colonisation of regenerating forest in the northern hemisphere suggests that individual species characteristics strongly influence plant distributions (Verheyen and Hermy, 2001). It seems likely that some species at Otatara are limited by dispersal, but that the majority are not.

The revised model (Figure 6. 2) does not incorporate the individual characteristics of weed species, which may be why the predicted outcomes of the model were not observed. The target species show individual and distinctive correlations with environmental variables. For instance, the percentage cover of *Montbretia* is unusual in being significantly negatively correlated with light availability (Chapter 5). This individuality implies that correlations involving aggregate measures of plant abundance may be weak because they represented the overall response of many species that, in fact, have different requirements for growth and dispersal capabilities. Similarly, correlations between residential development and weediness may not have been evident because species have distinctive responses to the effects of development.

Correlations involving individual species were also weak, but this might be because of the relatively small number of sites at which most species were present. Even the most abundant of the target species was present at only a third of all quadrats sampled.

The individuality of a species' responses to those environmental variables assumed to control dispersal and establishment has wider implications. This is sometimes used as an argument against the type of community-scale study conducted here (Lawton, 1999), echoing the 'individualistic' concept of vegetation proposed by Gleason in the early 20$^{th}$ century in opposition to the idea that a universal theory of succession could be derived (Miles, 1987).

Diverse responses were encountered here, and correlations may be weak as a result, but some generalisations can be drawn. In fact, many accepted principles of invasion are

generalisations based on probabilistic patterns (Lodge, 1993). For example, it is accepted that weed abundance is higher at forest edges, even though it is not possible to predict the precise magnitude of this effect (Table 2.1).

## 6.7 Summary

The composition of a plant community is the outcome of many episodes of invasion, 'natural' or associated with human activity. Lodge (1993) argued that three things dictate community composition: history, chance and determinism. This study has examined the possible role of determinism. There is no reliable way to identify the workings of chance but that is important in creating plant assemblages, and may be why the present study, and others like it, yield suggestions or generalisations rather than concrete laws.

Lodge (1993) discusses the role of the evolutionary history of an invaded community, but the recent history of the community is also important. At Otatara, the history of human modification of forest, such as past patterns of disturbance and propagule distribution could explain some variation in weed abundance that cannot be attributed to current spatial context or forest interior characteristics. This requires further investigation, particularly with regard to private individuals undertaking weed removal and thereby mitigating adverse effects of residential development.

This thesis relied on statistical tests to show correlation between variables. It cannot demonstrate causation. This type of observational approach is however, useful for generating hypotheses that can be tested by careful experimentation (Jesson et al., 2000). Thus, a key purpose of the model developed here is to suggest directions for future research. These, and practical suggestions for management, are the subject of the concluding chapter.

No clear relationship was found between the abundance of weeds within forest patches and residential development. This may be because research was conducted at a small spatial scale, or due to the contingent nature of invasion, which is also a product of chance and the biological characteristics of individual species. Empirical support was found, however, for the proposition that residential development alters (a) the structure of the forest edge and (b) interior conditions in ways that improve the chances of exotic plants spreading into the forest and successfully establishing within it.

# Chapter 7

# Conclusion and Recommendations

This thesis concludes that the abundance of environmental weeds in an area of forest is partly determined by its spatial context. Residential development changes the spatial context and, hence, interior conditions of nearby forest in ways that improve the likelihood of exotic plant propagules dispersing into the forest and reaching sites suitable for germination and growth. Hence, environmental weed abundance in forest patches is likely to be related to residential development in the adjoining matrix. This chapter begins by summarising findings that support this conclusion.

The relationship between the abundance of environmental weeds in forest and residential development is geographically variable: it is stronger at some measurement scales, and in some areas, than others. The latter variation is contingent upon the history of land use and forest modification, intensity and nature of development and the biological characteristics of the environmental weed flora. The model proposed here may not apply in every area and to all environmental weeds, a point to be clarified by further research, but given the necessity for effective management of environmental weeds and minimising the effect of suburban development in rural areas, it may still inform management to limit the effects of residential development that enhance weed invasion of indigenous forest.

This chapter advocates future research directions: to check if correlations observed at Otatara hold for other sites, whether or not the model proposed in Chapter 6 is useful, and to elucidate the role of factors such as management history. Research should be conducted at a range of spatial scales. This thesis has shown the advantages and limitations of research at a very local scale in contrast to research at a larger scale. Semi-experimental studies that measure the change in weediness of forest patches as development in the matrix progresses would ensure deeper understanding of the mechanisms proposed here.

# 7.1 Conclusions from the research at Otatara

The patterns evident at Otatara differ from those observed in other areas and at coarser spatial scales, yet support the widely proposed explanations for those large-scale patterns. A recent study related weed abundance in forest reserves to characteristics of nearby subdivision in coastal Northland (Sullivan et al., in prep.), and a comparison with findings from Otatara was revealing. Sullivan et al. - like overseas researchers (Chapter 2) - found strong positive correlations between the number of exotic plant species in forest and several indicators of residential development.

Those correlations were not evident at the small spatial scale of research at Otatara, but data collected there clarified mechanisms that could create the pattern observed at coarse scales. Firstly, abundance of environmental weeds proved to be correlated with characteristics of the forest interior:

- Environmental weeds are more abundant in lighter parts of the forest, although this correlation is not evident for all species.

- Environmental weeds are more abundant in places subject to anthropogenic disturbance, although, again, each target species showed a distinctive response to this factor.

Such correlations have been found in many studies made elsewhere (Chapter 2) and were expected to be apparent at Otatara. It was also shown that the forest interior environment is influenced by the spatial context of forest, particularly distance from the patch edge and edge structure:

- Intensity of anthropogenic disturbance tends to be greater closer to forest edges, and near more structurally open edges.

- The amount of light that penetrates the canopy tends to be greater near more open edges, although no trend with distance from the edge was detected.

Again, those findings were expected given reports in the literature regarding edge effects (Chapter 2). The research at Otatara also found the anticipated edge-related distribution of exotic plants:

- The abundance of environmental weed is higher toward forest edges.

- Environmental weeds are more abundant near more structurally open edges.

Those correlations were apparent when aggregate measures of weediness were analysed but were not always evident for each individual target species.

The innovative part of this study has been in developing evidence to support a model that explains the observed correlation between weed abundance in forest patches and nearby residential development. Broadly, two mechanisms underlie this correlation: one relating to dispersal opportunities for exotic plant propagules, the other to availability of suitable sites for establishment within the forest.

With regard to dispersal, this research has shown that residential development at Otatara does affect the number of known environmental weeds growing on properties adjacent to forest (older properties support more weed species), but this does not cause increased abundance of environmental weeds within the forest. Characteristics of the closest property may, however, be a poor measure of the weediness of the matrix. Given the ease of dispersal through the matrix, and the long period of naturalisation of most environmental weeds at Otatara, the effects of this process are likely to be more evident at a larger scale.

Residential development was found to be associated with conditions likely to enhance dispersal opportunities at the local scale:

- Increased openness of forest edge structure is associated with residential development; and

- Increased anthropogenic disturbance of the forest is associated with residential development and increased openness of edge structure.

These correlations suggest greater movement of people and other plant vectors into the forest at Otatara. They also support the second proposed mechanism whereby residential

development enables environmental weed invasion of forest patches; provision of sites for environmental weeds to become established within forest. As well as increased disturbance:

- Increased light availability within forest is correlated with greater openness of edge structure and age of residential development.

Such forest environmental characteristics are associated with increased abundance of environmental weeds.

## 7.2 Recommendations

Strategies for the management of conservation of indigenous vegetation and habitat on private land have been the subject of debate at a national level, and the findings of this thesis have implications for that debate (Chapter 1). This section will first discuss strategies for managing conservation in urbanising lowland areas at a national level before turning to specific ways in which local government and private landholders or interest groups could reduce the threat that environmental weeds pose to indigenous forest patchesin Otatara.

### 7.2.1 Implications for national biodiversity management

There has been some discussion over the direction of conservation strategies in New Zealand. Presently, there is confusion about who holds responsibility for conservation of indigenous vegetation and habitat on private land - a substantial portion of national biodiversity - (MfE, 2000). By default, management has devolved to local governments, which are wary of imposing strict conservation rules, discouraging development thus alienating ratepayers (Davis and Cocklin, in press). Thus, the Act is likely to result in loss of environmental amenities that do not have clear monetary value (Grundy and Gleeson, 1996). This thesis cannot address that conflict, but can advise about one ecological implication of marrying conservation and development.

Recent critiques of conservation management in New Zealand have identified a lack of clarity in the division of conservation responsibilities between Regional Councils and Territorial Local Authorities. This has potential to cause confusion at Otatara. In view of the links between intensified residential or urban development (managed at the local level) and the

environmental weeds (managed at the regional level) there is need for close communication between the two tiers of government.

The Southland Regional Council is the primary agent in environmental weed management, but its role on private land is limited. It may be involved in research to identify plants likely to act as environmental weeds, and creating and enforcing rules that apply to their sale or cultivation, but generally the onus is on landholders to carry out control. The results of this research suggest that there are often known weed species growing on private land adjacent to indigenous forest. This suggests that the status of such weeds should be better publicised, and perhaps that rules pertaining to those species like Chilean flame creeper should be made more rigorous. There are rules aimed to prevent 'containment plant pests' spreading onto neighbouring properties (Environment Southland, 2000). It may be appropriate to extend those rules to encompass known environmental weeds spreading into nearby indigenous forest.

The DoC is in a similar position. It has limited power to act in Otatara, but may be usefully involved in identifying potential environmental weeds and advocating their control. The two bodies also tender advice about environmental weed management to local councils or the general public and are more able than local councils to undertake research, typically having greater expertise and resources (Berke et al., 1999), so the information presented below is still relevant to those organisations.

Under present legislation, and after the changes advocated by the Ministerial Advisory Committee (MfE, 2000b), most responsibility for the matters discussed here falls to the local council and private landholders. Possible ways to minimise the threat environmental weeds pose to indigenous vegetation are outlined below.

## 7.2.2 Strategies for local government

Critics of the RMA have suggested that local councils may be uncertain about their role in biological conservation and lack the resources for effective management. This may be the case in many areas, but the ICC has a detailed database describing indigenous vegetation at Otatara and planning documents acknowledge the national significance of the area and place strict limitations on further forest clearance. Norton wrote: "it is considered likely that any further clearings will result in a reduction in the long term viability of the Otatara forest remnants and that no more clearings should be allowed" (1996, p25). The rules in the District plan do not forbid any further clearance, but it is a discretionary activity (ICC, 1998).

Those rules, even if rigorously applied, may not be sufficient to ensure the protection of indigenous forest from environmental weeds. This research suggests that residential development in the matrix adjoining forest may lead to enhanced weed invasion even when it is not associated with forest clearance. There is scope within the Proposed District Plan (ICC, 1998) for the Council to require that those wishing to undertake development take steps to mitigate its effects on indigenous habitat, and the suggestions below might be useful in that context.

The Invercargill District Plan states that all subdivision and building construction which are likely to significantly affect forest at Otatara are discretionary; that is, a proposal needs to be considered by a Council officer before permission is granted and one of the matters to be considered in granting consents is "infestation by exotic fauna and flora" (ICC, 1998, p115). The consent-granting officer can require the applicant to take steps to mitigate such effects. In view of the information presented here, mitigation requirements might include such conditions as: that the forest edge is not subject to disturbance during house construction, and that after development the edge is to be fenced, or sealed with a hedge of indigenous species, to reduce traffic into the forest.

Financial assistance in the form of fencing grants is offered by several local councils (Froude, 1997) and is in keeping with the non-regulatory approach emphasised in the report of the Ministerial Advisory Committee (MfE, 2000b). The Invercargill District Plan mentions the provision of financial assistance and advice and information about conservation issues to landholders as methods for achieving conservation objectives. The following section suggests specific actions to be promoted at Otatara.

### 7.2.3 Actions by individuals

There is a widespread understanding that management of forest patches necessitates management of the forest edge and adjoining matrix (Gascon et al., 2000). It is clear that weed abundance in forest patches at Otatara is affected by edge structure, so that managing the edge is likely to reduce weed invasion. One of the most effective ways to preserve indigenous forest on pastoral land is to fence remnants to encourage regeneration of indigenous species, which are suppressed by grazing and trampling (Burns et al., in press; Norton and Miller, 2000). Removal of periodic disturbance by grazing also decreases opportunities for weed establishment (Burns et al., in press).

Fencing would also be an effective way of managing forest adjoining residential properties where grazing is not a concern. Fences limit traffic through the edge into forest and so prevent the spread of exotic species carried by people or animals. Fencing also reduces the intensity of anthropogenic disturbance, and allows the edge vegetation to close up with bushy lateral growth.

Environmental weed abundance is lower where edges are structurally closed. Gascon et al. (2000) suggested that tropical forest remnants could be preserved by creating a buffer of uncultivated land between cultivated areas and forest, to soften the edge and reduce edge effects. A similar technique could be pursued at Otarara by planting indigenous species in hedges or borders at edges created a structurally closed edge. For example the edge bordered by flax in Figure 3.2 (C) has been sealed by deliberately planted vegetation. Other indigenous species, such as *Pittosporum* spp., may be appropriate for such planting.

Weed abundance within forest is correlated with anthropogenic disturbance and increased light availability. Human use of forest close to residential areas could be limited in ways that reduce anthropogenic disturbance and allow canopy regeneration (to reduce light availability). It is probably unacceptable to forbid access to forest in an area like Otatara, but the fact that some activities encourage weed invasion and should be limited.

Garden rubbish dumping introduces environmental weeds to the forest and should be avoided. Similarly, damage to the existing vegetation and major soil disruption are likely to provide sites for weed establishment. Non-intrusive activities like walking seem less likely to have deleterious effects. It may, however, be profitable to limit walkers to defined tracks. The areas around tracks can then be easily targeted for weed control.

This study did not investigate the effects of attempts at weed control by local property owners or other agencies, but this seems to likely to reduce the abundance of environmental weeds. In view of the patterns found here, those undertaking such control should target places close to forest edges, sites of known disturbance, and high light environments as those areas are most likely to be infested.

## 7.3 Further research directions

Principles of landscape ecology - for instance derived from the equilibrium theory of island biogeography - have been applied to conservation planning since their inception (Diamond, 1975). Concern has been expressed that landscape ecology is too reliant on theory, and does not always yield conclusions backed up by field observation or experiments, which limits its applicability for management (Simberloff, 1997). Inferences drawn from landscape ecology - for instance regarding the negative effects of urban development on indigenous forest - need to be supported with empirical observations, but at the same time it may not be possible to collect detailed information regarding every species or habitat type of conservation interest.

Weed invasion typifies this problem. It is difficult to make generalisations about weed invasion because it is controlled by the characteristics of individual species and habitats. Some authors have suggested that detailed understanding requires close examination of the interaction between each weed species and a particular environment (Buist et al., 2000). However, the applicability of such specific information to management decisions made at a regional level or higher would be limited, and the costs of collecting data would be great. Thus, an intermediate level of study is required, to support theory with empirical results. That approach has been taken in this thesis.

It has been suggested that studies relating weed invasion to human activity need to be conducted at a range of spatial scales (Vila and Pujadas, 2001). This thesis has contributed to that by focusing on a local scale to compliment existing research at coarser scales. There is still need for further research, and at many scales, to capture details of the interactions of weed invasion and changes in land use.

Research should also be conducted in different areas to gain a deeper understanding of the composition of the weed flora, its dispersal mechanisms, and requirements for germination and growth. Community-based research would also clarify the role of the indigenous species composition of the indigenous biota, which was not considered here but may be influential. Other factors that warrant further investigation are the history of forest patches and the role of local residents or landholders in weed control. The poeration of those factors is more likely to be evident at fine scales of research (like that used here) than at coarse scales.

Vila and Pujadas (2001) suggest that weed invasion research should be conducted at a range of temporal scales. One of the acknowledged limitations of the research design used here is its use of different ages of development as a proxy for increasing time since development, which may not be accurate. This means that the theory proposed here, although reasonable and supported by data collected in the field, cannot be validated. That would only be possible with experimental manipulation of sites where time is a controlled factor. Experimentation on weed invasion of indigenous habitats is ethically questionable, but a pseudo-experimental research design could be developed using a reliable series of data describing forest patches at different stages of development in the matrix. For instance, Timmins and Williams (1991) based their research on data describing forest and scrub reserves New Zealand-wide from the Biological Survey of Reserves, conducted mostly in the 1870s and 1980s. If those sites were re-surveyed now, a comparison across time could be made of weed abundance within reserves, in relation to change in land uses surrounding reserves. This would be at a coarse scale. At a local scale, appropriate data could be gathered by surveying and re-surveying a set of permanent plots (after Wiser et al., 1998). Such plots have not been established at Otatara. However, the relatively detailed survey conducted by Bill and others (Bill, 1999) might provide an adequate base line for future research, if residential development continues in Otatara.

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# Appendix A

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